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AN ENDEMIC RADIATION OF HYDROBIID SNAILS FROM ARTESIAN SPRINGS IN NORTHERN SOUTH AUSTRALIA: THEIR TAXONOMY, PHYSIOLOGY, DISTRIBUTION AND ANATOMY

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CONTENTS

ABSTRACT

Artesian springs between Marree and Oodnadatta contain an endemic fauna of hydrobiid snails that have undergone an adaptive radiation in which habitat partitioning and size displacement are clearly evident. Ten new species in two new endemic genera, *Fonscochlea* and *Trochidrobia,* are described. Three of the species of *Fonscochlea* are divided into a total of six geographic forms, which are not formally named. Two geographic forms are restricted to single springs, the remainder being found in several springs, spring groups, or complexes of springs. *Fonscochlea* is divided in to two subgenera, *Fonscochlea* s.s. containing five species and *Wolfgangia* with a single species.

Both genera are represented in most springs, with up to five taxa present in single springs in the Freeling Springs Group and in some of the other springs in the northern part of the spring system. As many as four taxa are present in most other springs. The pattern of one or two sympatric species of *Trochidrobia,* a large, amphibious species of

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Fonscochlea, one large aquatic species of *Fonscochlea* and a small aquatic species of *Fonscochlea* is established in most of the springs in the area. Some of the factors leading to the evolution and maintenance of this diversity are discussed.

A subjective classification, based on shell, opercular and anatomical characters, was tested phenetically using discriminate analysis.

Simple physiological experiments were carried out on some of the taxa to test for the effects of temperature, submergence, desiccation, increased salinity, reduced dissolved oxygen, and responses to light. All taxa showed a wide range of tolerance to salinity and temperature but the small animals were more susceptible to desiccation than the large ones. Varying responses to light and submergence were obtained but all taxa showed reduced activity in deoxygenated water.

The anatomy of the type species of both genera is described in detail. *Fonscochlea* is unique in having two equal-sized sperm sacs in the female that are probably derived from the bursa copulatrix and, as in *Trochidrobia,* which has a single sperm sac, the seminal receptacle is lost.

The endemic snails, together with the unusual endemic crustaceans sympatric with them, and their unusual community structure, give the springs special interest, both from the scientific and conservation viewpoints.

Key words: Mollusca, Hydrobiidae, springs, endemics, taxonomy, physiology, anatomy, speciation, sympatry, habitat partitioning

INTRODUCTION

The most nearly permanent type of water body in an arid environment is probably an artesian spring (Naiman, 1981). The habitat provided by an artesian spring in this situation is analogous to that of an island. Each spring is typically separated by arid land providing as marked a discontinuity of habitat as the sea does to terrestrial organisms. Artesian springs are typically permanent, within a moderate time scale, perhaps in the order of thousands to even millions of years for spring systems but tens to hundreds of years for individual springs, and usually provide a reasonable diversity of habitats. Given these conditions one might expect genetic differentiation of populations in separate springs and some habitat partitioning allowing similar species to coexist. Studies of the faunas of arid-zone artesian springs have sometimes revealed spectacular examples of speciation and habitat partitioning. The best documented examples are of the fishes of the western deserts in the United States and northern Mexico (Minckley, *et al.,* 1986), particularly of the Death Valley system (Soltz & Naiman, 1978). Studies of these fishes have provided insight into the nature of the speciation process (Turner, 1974; Soltz & Hirshfield, 1981), biogeography relative to drainage history (Hubbs & Miller, 1948; Hubbs *et al.,* 1974; Smith, 1978) and adaptation to diverse spring-fed habitats (Naiman & Soltz, 1981).

Natural water bodies in arid lands, such as springs, water in caves and marshes, are frequently refugia for relict biota. There are numerous examples, particularly amongst fishes and crustaceans, that are well documented. A spectacular example is the crocodiles in pools in the Ahaggar Mountains of Africa, now surrounded by vast desert areas (Cole, 1968). Springs sometimes support diverse faunas that might be partly relictual and partly endemic radiations. The hydrobiid snails of the Cuatro Cienegas Basin, Coahuila, Mexico, are presumably an example of such a fauna (Taylor, 1966a; Hershler, 1984, 1985).

Radiations of hydrobiid snails in springs in temperate climates are also known, examples including those in Florida (Thompson, 1968) and parts of Europe (e.g., Radoman, 1983). A spectacular radiation of the related family Pomatiopsidae in Southeast Asia has been well documented by Davis (1979).

Bayly and Williams (1973) note that extremely little is known about the biology of Australian springs. This is certainly true for the artesian springs associated with the Great Artesian Basin. Before this study commenced the only animals that had been studied in detail in artesian springs in arid Australia were the fishes (Glover & Sim, 1978a; Glover, 1982). Recent biological work is summarised by Ponder (1986).

The artesian springs in the arid north of South Australia (Figs. 1, 2) were only recently shown to contain a large and interesting biota (Mitchell, 1985; Symon, 1985; Ponder, 1985, 1986). To date the only invertebrates described from these mound springs are a phreatoicid isopod (*Phreatomerus latipes* (Chilton, 1922), an ostracode, *Nagarawa dirga* (DeDeckker, 1979), and a macrostomid flatworm, the first record of this order from Australia (Sluys, 1986). Both of the Crustacea are endemic to the springs and belong in monotypic subfamilies.

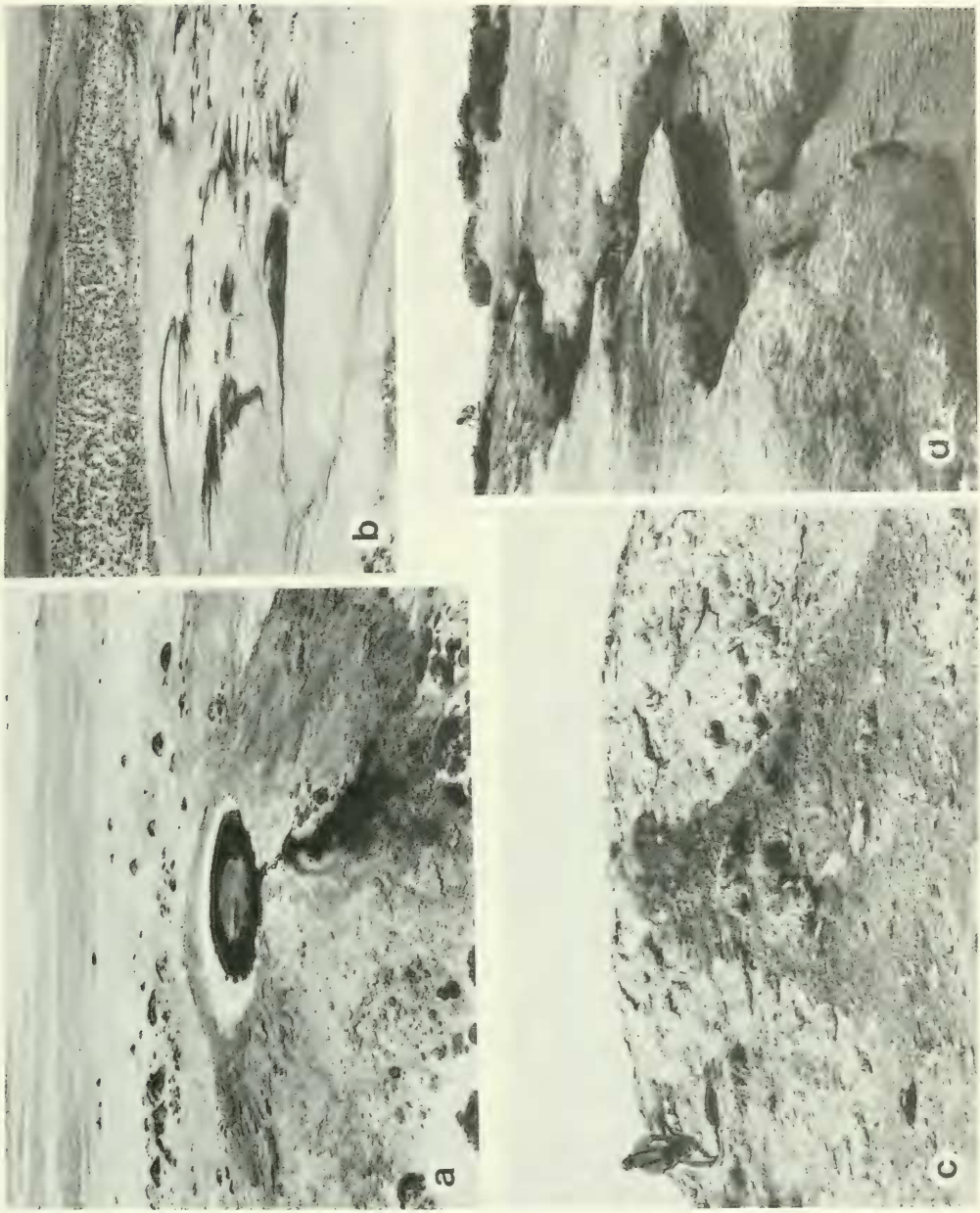

FIG. 1. Various springs in the Lake Eyre Supergroup showing some of the morphological diversity.
A. Blanche Cup Spring (Stns 8–12), a conical, calcareous mound spring with a crater-like pool.
B. Aerial view of part of Hermit Hill Spring Complex showing part of a spring group (Finniss Swamp West) composed of small ground-level springs and some low sand mounds.
C. Almost extinct mound in the Blanche Cup Complex, in the Horse Spring Group (stn 748). Snails and crustaceans are abundant in small seeps such as this.
D. The Bubbler Spring (stns 13–17), one of the largest flows in the Lake Eyre Supergroup.

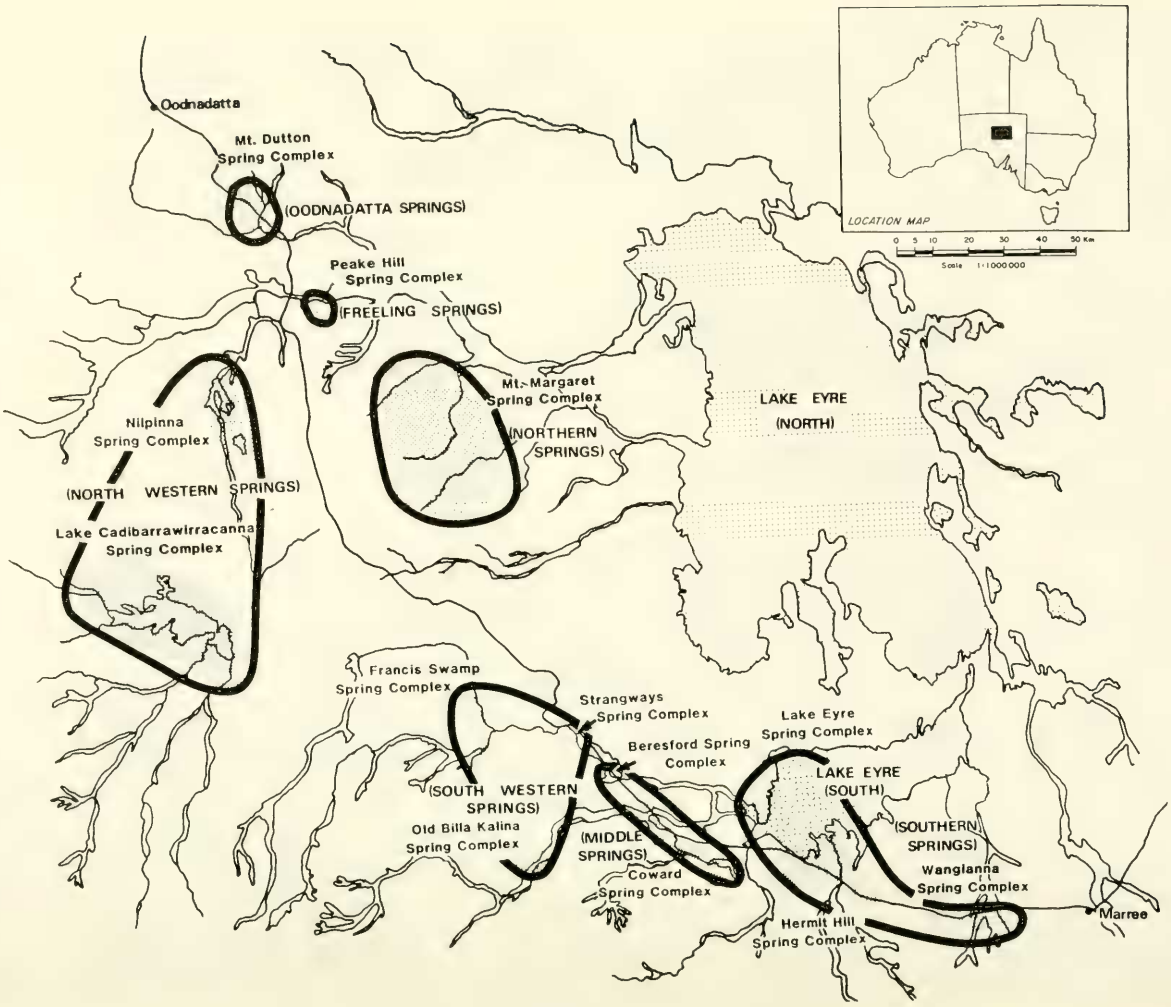

FIG. 2. The major spring complexes in the Lake Eyre Spring Group.

Gastropod molluscs were reported from the mound springs by Mitchell (1980, unpublished; 1985) who, on the advice of Dr. B. Smith, to whom the material was sent for identification, recognized the presence of three or possibly four species referable to three or four genera. DeDeckker (1979) also refers to these snails as undescribed endemics, on Smith's advice. We cannot find any earlier references to these species in the literature, despite their being conspicuous and abundant in most of the springs. A few of the early explorers noticed the small fish found in some springs (see review by Glover & Sim, 1978b).

Some of the more accessible mound springs were visited in the latter part of the 1970's by several biologists who made some collections, those of W. Zeidler of the South Australian Museum being the most significant. His collections and those sent to Dr. B. Smith were made available to one of us (W.F.P.) and field work was carried out in 1981 by W.F.P. and Zeidler. The result of that field investigation, and an additional one the same year by Zeidler, showed the existence of an apparent endemic fauna of hydrobiid snails of considerable diversity.

The available information on the mound-spring fauna was reviewed in an Environmental Impact Statement (E.I.S.) for the Olympic Dam Project (Kinhill-Stearns Roger, 1982) and in a supplement to this E.I.S. (Kinhill-Stearns, 1983). The review in the supplement included some new information on the hydrobiid snails provided by two of us (W.F.P., B.W.J.). Because the Olympic Dam Project required water from a borefield located near a large spring complex at Hermit Hill (Fig. 2; Appendix 1, Fig. 62), further biological and hydrological studies were carried out to assess the importance of the flora and fauna associated with these springs. This paper has been developed from the report resulting from those studies. A summary of the results of the hydrobiid work appears in the report prepared for Roxby Management Services on the mound springs (Ponder & Hershler, 1984).

The importance of the springs and the need for their conservation has been stressed by Casperton (1979), Harris (1981), Symon (1985) and Ponder (1985, 1986). This view has also been strongly supported by the evidence accumulated in the reports prepared as a result of the Olympic Dam Project (Kinhill-Stearns Roger, 1982, Kinhill-Stearns, 1983, 1984). The World Wildlife Fund has recently provided funds to fence some springs.

The snails present in the mound springs are members of the Hydrobiidae, a worldwide family of prosobranch gastropods that are part of the large, predominantly marine superfamily Truncatelloidea. The hydrobiids were probably derived from brackish-water ancestors in the middle part of the Mesozoic (Ponder, 1988) and some members of the family are still restricted to brackish-water environments. To date the family is known to be represented in Australia by about nine genera and approximately 35 named species, excluding those from the mound springs, although recent unpublished work by W.F.P. shows that this fauna is actually much larger.

The adaptations of organisms to the diverse and often extremely harsh aquatic environments in deserts are of interest to physiologists as well as ecologists and evolutionary biologists. While a variety of taxa are usually found in such waters, only the desert fishes are well studied in terms of their ecology and physiology (see summaries, Deacon & Minckley, 1974; Soltz & Naiman, 1978; Naiman & Soltz, 1981). In areas in which hydrobiid snails have radiated extensively in desert waters, particularly spring systems of North and Central America (Taylor, 1966a, b; Hershler, 1985; Hershler & Landye, 1988) and Australia (Ponder, 1986), their frequent local diversity and high densities suggest that they are trophically important members of desert aquatic communities. Yet there is a paucity of data concerning their ecology and virtually nothing is known of their physiology. Tolerances to the environmental parameters that often achieve extreme levels in desert waters (e.g., salinity, temperature), have not been studied for any spring-dwelling hydrobiid species, although some work on South African species of *Tomichia,* of the related family Pomatiopsidae, has been done (Davis, 1981).

This paper commences with an introductory section outlining the main features of the mound springs. The rest of the paper is divided into three sections. The first deals with the taxonomy of the hydrobiid snails, followed by a detailed account of the anatomy of the type species of the two genera found in the springs. The results of the physiological work done in the field are presented in the third section.

The mound springs—a brief description

Geomorphology and water chemistry: The artesian mound springs of South Australia are aligned in an arc running from the far northern

part of the state at Dalhousie Springs, north of Oodnadatta, around the south of Lake Eyre to Lake Frome and Lake Callabonna on the eastern side of the Flinders Ranges. Additional artesian springs are found in western Queensland and were found in the north-west of New South Wales, but these are now mostly extinct (personal observations by W.F.P. and M.A. Habermehl, pers. comm.), presumably as a result of water extraction from the basin by the pastoral industry. The springs are natural discharges from the aquifers formed from the Jurassic and Cretaceous sedimentary rocks of the Great Artesian Basin (see Habermehl, 1980, 1982, for geological details). They occur in a variety of forms, the most common being small mounds resulting from groundwater precipitates, mainly carbonates, and fine sediments derived from the aquifer and confining beds. Wind-blown debris and plant material also contribute to the mound formation. The mounds are composed primarily of hard travertine or of sediment, or layers of both. They range from virtually flat to large mounds several tens of meters high. The larger mounds are the older springs, the ground-level springs the youngest (Ponder, 1986: Fig. 4). More detailed descriptions of the springs are provided by Watts (1975), Habermehl (1982), Thomson and Barnett (1985), and Ponder (1986). The South Australian mound springs are the most active and numerous of the artesian springs fed by the Great Artesian Basin (Habermehl, 1982) and are now the best known biologically. The little that is known of Queensland artesian springs is summarised by Ponder (1986).

Dalhousie Springs, to the north of Oodnadatta, yields about 95% of the natural discharge from the Great Artesian Basin in South Australia (Williams, 1979; Williams & Holmes, 1978). These springs are, however, outside the present study area, as are some small springs east of Marree to the north and east of the northern Flinders Ranges. Some of these springs contain endemic invertebrates, including hydrobiids, and these will be dealt with elsewhere. The springs included in this report (Fig. 2; Appendix 1) are located mainly on the Warrina, Billa Kalina and Curdimurka 1:250,000 map sheets and a few on the Oodnadatta sheet. They form a zone about 400 km long and as much as 20 km wide between Marree and Oodnadatta (Fig. 2) and are referred to as the Lake Eyre group by Habermehl (1982) and the Lake Eyre Supergroup by Ponder (1986).

The morphology of the springs in the Lake Eyre Supergroup is diverse (Fig. 1). The springs range from surface seeps (Fig. 1b) to low, conical mounds (Fig. 1a, c) or even small hills. The mounds consist of sand, silt and clay, often cemented by carbonate and overlain by layers of carbonate (Habermehl, 1980, 1982). The cemented mounds often persist for considerable periods after the springs that formed them have ceased to flow, but the unconsolidated mounds erode rapidly. Some mounds have a crater-like, water-filled depression at the top (Fig. 1a), while others have rounded domes (Fig. 1c); both types typically have one or more outlets. Some of the larger, dome-like mounds (e.g., Kewson Hill and the Elizabeth Springs mound) have several small seeps issuing from them.

Discharges from most of the springs are small, ranging from about 0.5 litre per second to 7.5 litres per second at the Bubbler Spring (Fig. 1d) (Cobb, 1975; Williams, 1979; Habermehl, 1982). Despite this, discharge from some springs is sufficient to maintain flows for several hundred metres or, more rarely, a kilometre or more, providing a well-vegetated wetland habitat. Other springs have such a small discharge that they do not maintain an outflow, having only a pool or small swampy area at the head. Others are merely permanently damp patches that might flow occasionally. Some small springs in the Hermit Hill complex (Fig. 1b) have been observed flowing on some occasions and are dry on others. The Lake Eyre Supergroup has a total estimated discharge of 100–200 litres per second (Habermehl, 1982), compared with 670 litres per second for Dalhousie Springs (A.F. Williams, 1974; Williams & Holmes, 1978).

The depth of the water in the pools and outflows rarely exceeds 2–3 cm and is usually only a few millimetres. The pools and outflows usually contain sedges but rarely true aquatic vegetation apart from algae. The outflows are usually narrow trickles with a firm, sandy base and, in the case of the hard mounds, calcareous rock.

Our observations indicate that the area of outflow diminishes in summer, presumably owing to increasing evaporation, and some observations suggest that periods of high barometric pressure coincide with reduced water flow (C. Woolard, pers. comm.).

Williams and Holmes (1978) have estimated that a spring with a small discharge typical of many of the springs in the Lake Eyre

Supergroup, shown on the Curdimurka map sheet, would take about 1000 years to deposit sufficient calcium carbonate to build a hemispherical mound three metres high. On this basis some of the larger mounds, such as Kewson Hill, might, even with substantially increased flow rates, take several tens of thousands of years to form. Forbes (1961) has shown, however, that drilling on mounds in this vicinity reveals that a substantial portion of the mound is formed by the deposition of sand and clay rather than "limestone", suggesting that the calculations by Williams and Holmes (1978) might be invalid.

Analyses of the water from the springs in the Lake Eyre Supergroup have been given by Cobb (1975), Williams (1979) and Kinhill-Stearns (1984) and summarized by Habermehl (1982). Sodium and bicarbonate are the major ions in springs in the eastern part of the Lake Eyre group whereas in springs in the western part the bicarbonate component is small and sodium and chloride ions predominate over calcium and sulphate. Total dissolved solids in most springs range from 2000–4000 ppm, with a few in excess of 5000 ppm, and pH from about 7.1 to 8.1, although a field pH of up to 9.95 has been recorded in recent surveys. The temperatures in the spring vents are constant throughout the year and show a slight increase from east to west ranging from upper teens to mid-twenties (°C) in the east to upper twenties in the west. The salinity increases toward the discharge areas of the Great Artesian Basin.

A few springs in the Lake Eyre Supergroup might not originate from the waters of the Great Artesian Basin aquifer, or show significant mixing with sulphate-rich ground-water, as their hydrochemistry is atypical. These springs are located on the faulted edge of the basement rocks and include Kerlatroaboorntallina Spring, Talton Springs, Edith Spring, Dead Boy Spring and Pigeon Hill Springs, the last two in the Hermit Hill Complex. None of these springs contains the typical mound spring invertebrates.

Exploitation of the water from the Great Artesian Basin has resulted in a drop of the potentiometric surface by several tens of metres in heavily developed areas (Habermehl, 1980). Even by the turn of the century the sinking of bores near some springs had greatly reduced or extinguished their flow (Pittman & David, 1903).

At present, a new steady-state condition appears to have been reached in which total recharge and discharge are approaching equilibrium again (Habermehl & Seidel, 1979; Habermehl, 1980), and little change is expected to occur in the discharge rates of the springs provided no new well development takes place.

Spring groups and complexes: The mound springs in the Lake Eyre Supergroup are not distributed evenly and for the purposes of this report can be divided into several major spring complexes. Within each of these complexes spring groups can be identified. A spring complex can be defined as a large cluster of springs separated from adjacent spring clusters by several tens of kilometres. Smaller groups of springs, either within a complex or an isolated group, can be referred to as spring groups. For example, Hawker Springs can be called a spring group within the Mt. Margaret Spring Complex. In the Hermit Hill Spring Complex there are several spring groups, e.g., Finniss Swamp West (= West Finniss), Hermit Hill Springs Proper and Old Woman Springs. The following classification of spring complexes in the Lake Eyre Supergroup is essentially that proposed by Kinhill-Stearns (1984) (Fig. 2). Table 1 lists the springs, grouped in complexes, containing hydrobiids.

To facilitate discussion we have arranged these spring complexes into seven informal systems (Fig. 2), the arrangement being biased towards the distribution of the hydrobiid fauna. Detailed maps for each spring area are given in Appendix 1 and these are referred to in the list below.

1. The Oodnadatta Springs.

Mt. Dutton Spring Complex. The few small springs on the Oodnadatta Map Sheet that lie southeast of Oodnadatta (Appendix 1, Fig. 63).

2. The Freeling Springs:

The Peake Hill Spring Complex. Includes the Freeling Springs and a few small springs to the north and northwest of Mt. Denison (Appendix 1, Figs. 58, 63B).

3. The Northern Springs:

Mount Margaret Spring Complex. Includes the large, scattered group of springs to the east of Mt. Margaret, as well as the Peake and Denison Ranges (Appendix 1, Fig. 59).

4. The North Western Springs:

a) Nilpinna Spring Complex. A few scattered, small, springs to the west of the Marree-Oodnadatta Road and west of the Mt. Margaret Spring Complex (Appendix 1, Fig. 58).

TABLE 1. Distribution of taxa in springs and spring complexes. x = present (living), s = shells only

SPRING OR SPRING GROUP	*F. zeidleri* form A	*F. zeidleri* form B	*F. aquatica* form A	*F. aquatica* form B	*F. accepta* form A	*F. accepta* form B	*F. accepta* form C	*F. variabilis* form A	*F. variabilis* form B	*F. variabilis* form C	*F. billakalina*	*F. conica*	*T. punicea*	*T. smithi*	*T. minuta*	*T. inflata*	SPRING COMPLEX
Southern Springs																	
Welcome group	x				x							x	x				Wangianna
Davenport group	x				x							x	x				Spring Complex
Old Woman group	x					x						x	x				
West Finniss group	x					x						s	x				
Hermit Springs group	x					x							x				
Old Finniss group	x					x							x				Hermit Hill
Dead Boy Spring						x							x				Spring Complex
Sulphuric group						x							x				
Bopeechee Spring						x							x				
Venable Spring	s					s						s	s				
Priscilla Spring	s					s						s	s				Lake Eyre
Centre Island Spring	s																Spring
Emerald Spring							x										Complex
Middle Springs																	
Horse East group	x		x									x	x				
Horse West group	x		x									x	x				
Strangways Spring	x		x									x	x				
Mt. Hamilton Spring	x		x										x				Blanche Cup
Blanche Cup group (785, 787)	x		x									x	x				Spring
Blanche Cup Spring	x		x					x					x				Complex
Blanche Cup group (786)	x		x					x					x				
Little Bubbler Spring	x		x					x					x				
The Bubbler Spring	x		x					x					x				
Coward Springs Railway Bore	x							x									
Coward Springs group	x		x									x	x				
Kewson Hill group	x		x									x	x				Coward Spring
Julie group	x		x									x	x				Complex
Elizabeth group	x		x									x	x				
Jersey group	x		x									x	x				
Warburton group	x		x									x		x			Beresford Spring
Beresford group	x		x									x		x			Complex
South-Western Springs																	
Strangways group	x		x								x			x			Strangways Spring Complex
Billa Kalina group	x		x								x			x			Old Billa Kalina
Fenced Spring	x		x								x			x			Spring
Welcome Bore Spring	s										s						Complex
Margaret Spring	s		s								s			s			Francis Swamp
Francis Swamp group	x		x								x			x			Spring
Loyd Bore spring	x		x								x			x			Complex
Northern Springs																	
Brinkley Spring	x		x											x			
Hawker group	x		x						x					x			
Twelve Mile group	x		x						x					x	x		Mt. Margaret
Outside group	x		x						x					x	x		Spring
Fountain group	x		x						x					x	x		Complex
Big Perry Spring	x		x						x					x	x		
Spring Hill Spring	s																
Freeling Springs																	
Freeling group	x			x						x					x	x	Peake Hill Spring
North of Freeling Spring															x		Complex
Oodnadatta Springs																	
Big Cadnaowie		x															Mt. Dutton Spring Complex

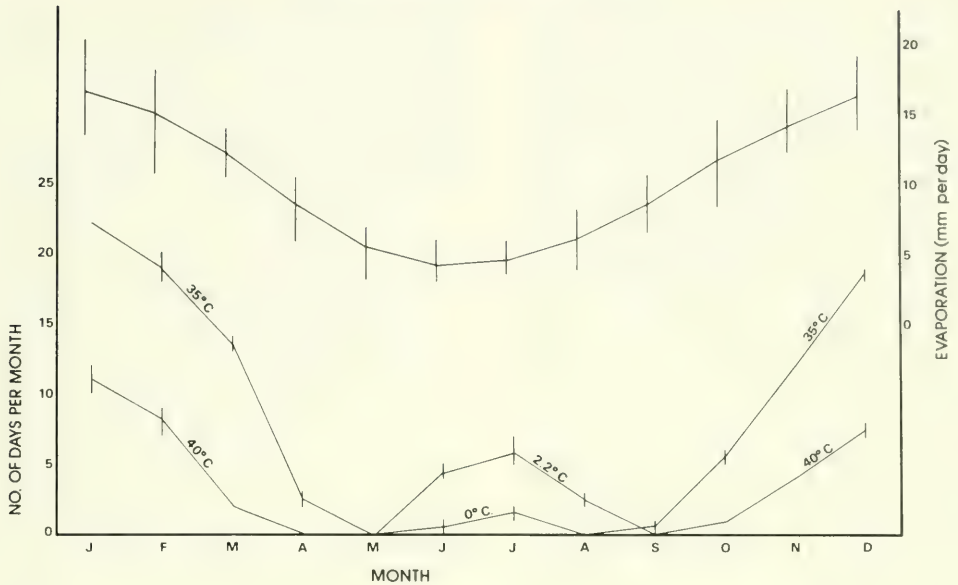

FIG. 3. Temperature and evaporation data for Marree and Oodnadatta. Mean daily evaporation, for each month, is given only for Oodnadatta, 1968–1982. The temperature data are for Marree, 1957–1982, and Oodnadatta, 1940–1982 together (with error bars indicating the range that the two encompass) and consists of number of days/month with temperatures >40° C., number of days/month with temperatures >35° C., number of days/month with temperatures <0° C., and number of days/month with temperatures <2.2° C.

b) Lake Cadibarrawirracanna Spring Complex. A widely scattered group of springs west of William Creek; the most westerly of all the spring complexes (Fig. 2; Appendix 1, Fig. 58).

5. The South Western Springs:

a) Francis Swamp Spring Complex. A large group of springs south of William Creek (Appendix 1, Fig. 60).

b) Old Billa Kalina Spring Complex. A scattered group of springs south of Francis Swamp on the northern side of Margaret Creek (Appendix 1, Fig. 60).

c) Strangways Spring Complex. A compact group of mostly extinct carbonate mounds to the east of Francis Swamp (Appendix 1, Fig. 59).

6. The Middle Springs:

a) The Beresford Spring Complex. Two main springs associated with two very large, extinct mounds, North and South Beresford Hills (Appendix 1, Figs. 60, 61).

b) Coward Spring Complex (Appendix 1, Fig. 61) includes the springs between Coward Springs and Hamilton Hill.

7. The Southern Springs:

a) Lake Eyre Spring Complex. A few springs on the southern and southwestern sides of Lake Eyre South and on islands in this lake (Appendix 1, Figs. 61, 62).

b) Hermit Hill Spring Complex. Several large groups of springs in the vicinity of Hermit Hill (Appendix 1, Fig. 62).

c) Wangianna Spring Complex. Includes the Welcome and Davenport Spring Groups, as well as the degraded Wangianna Spring (Appendix 1, Figs. 62, 63B).

Climate: Basic meteorological data for this region are presented in Fig. 3. Note the frequency of summer days with >40° C temperatures. Annual rainfall at Marree varied from 39.3–379.9 mm for the 21 years between 1957–1982, and at Oodnadatta from 54.3–465.8 mm for the 20 years between 1958–1982. Evaporation is exceedingly high, usually >10mm/day (Fig. 3) and, for a given year, typically exceeds precipitation by a factor of 10 or more (data for Oodnadatta and Marree were provided by the Bureau of Meteorology).

MATERIALS AND METHODS

Taxonomy

Taxonomic rationale: Because the mound springs are isolated from one another, each population has the potential to contain a unique genome that, given sufficient time, isolation and selective pressure, could develop into separate taxa. It was impractical to analyse all populations but a representative, non-random selection (Appendix 2, Tables 18–21) was made and these populations were treated as separate units in the statistical analyses to prevent bias towards the initial subjective split into species units.

The method that we have used to distinguish taxa is essentially phenetic. The phenetic grouping of populations by discriminate analysis is used as an aid for recognizing taxa but because strict acceptance of phenetic classifications, we believe, can be misleading, a subjective element was also introduced, generally on the side of caution. The rather large number of characters measured were statistically tested for differences between the recognised taxa. Most taxa are distinguished by at least one major set of characters (e.g., opercular, shell or reproductive) that are statistically significantly different ($p < 0.01$) from the phenetically closest taxon. It is our belief that the classification that we present is conservative and in all probability, by using techniques such as electrophoresis, genetic differences not easily recognised in the phenotype will be detected, and additional subdivision required. An electrophoretic program is planned that will test the classification adopted here and investigate some of the questions raised in the discussion.

Cladistic methods were not applied in this study because species discrimination depended largely on measurements, which would lead to difficulty in adequately defining character states.

Thorpe (1976) has discussed the practical and theoretical problems involved with sampling and analysing the phenetic differences among populations. He points out that there are two aspects to the problem of sampling, obtaining enough specimens to take account of local variation and surveying enough localities to represent the geographical area under consideration. We believe that our samples come close to meeting these requirements, especially as far as the shell and opercular data are concerned. Certainly the amount of variance obtained in most characters within even the wider-ranging taxa is generally small.

There are some inherent problems in working with hydrobiids because their shells are simple, unicoloured, rather featureless and small. Measurements of a number of shell parameters provide a picture of the shell that can be statistically analysed to detect subtle differences that occur between taxa. The opercular characters of species of *Fonscochlea* have proved to be useful. The number and relative development of the pegs on the inner surface of the operculum are the most useful opercular characters. These pegs are apparently a mechanism to increase the surface area for the attachment of the columellar muscles. The anatomical characters were much more difficult and time-consuming to study and, consequently, smaller numbers of individuals were examined. Important and obvious anatomical differences occur between the species of *Trochidrobia,* but within the two primary groups of *Fonscochlea* the anatomical differences are small and show high variance. Non-quantified characters, such as the pigmentation patterns on the head, were considered when constructing our classification, although in some taxa head-foot pigmentation showed considerable intra- and inter-population variation. Ratios were calculated using a number of measurements in all three data sets of shell, operculum, anatomy, in an attempt to reduce size-dependent differences and generate shape variables. These were used in the initial screening of the data to assist with the delineation of taxa.

Species are recognized in those cases in which, first, there were one or more morphological differences, which we judge to be significant, between the individuals in one taxon compared with the most similar taxon, and/or second, the taxa, recognisable by one or more differences, are sympatric and congeneric. Sympatric in this sense is used to include taxa living not only within the same spring but in closely associated springs (within a few hundred metres) in the same spring group (i.e. parapatry).

Subspecies have not been recognised but geographic forms have been identified where, within a taxon recognised as a species, there are one or more differences judged to be of significance between allopatric populations, i.e. from different spring groups. These forms are apparently of infraspecific status but whether they should be formally named must

await an analysis using biochemical methods. Nevertheless we have set out a formal diagnosis and description of each of these forms so that future investigation can more readily focus on some of the more important geographic differences that occur in the species that we recognise. In each case in which more than one form is recognised, form A is the typical form.

Materials: Specimens were collected by sifting sediment with a plastic hand sieve having a mesh size of approximately 1 mm, and by washing vegetation and solid objects (stones, bones, wood) into a bowl. Sieve contents were tipped into a bowl and excess water drained out. Snails and crustaceans usually sank to the bottom of the bowl and were collected in bulk. Although care was taken, some of the crustaceans, but very few molluscs, were lost during this process by their floating out with the excess water. The material was preserved in 5–10% formalin neutralised with excess $NaHCO_3$, after relaxation with menthol crystals for 10–12 hours.

For most springs, separate collections were taken at the head of the spring, at the upper part of the outflow, and at the middle part of the outflow. Collections were also often taken at the lower outflow and elsewhere, depending on the type and size of spring and amount of time available. Separate samples were sometimes taken from the water edge and middle of the flow, otherwise the sampling combined these zones.

Before sorting, samples were sieved in the laboratory through a 1 mm mesh to minimize any size bias produced by use of hand sieves during collecting. Samples were sorted under a low-power binocular microscope. If the sample was especially large, it was subsampled by removing all animals from a portion of the sample after thorough mixing, until a maximum of 600 individuals of any one species had been counted. The specimens were sorted into species and the counts of number of individuals for each species were used to give approximate percentage frequencies. Adults and subadults only were used in the percentage frequency analyses as identification of juveniles to species was difficult and time-consuming. Empty shells were ignored in counting. The results obtained by the analyses of qualitative samples have several limitations that are discussed below.

Most of the material on which this report is based is housed in the Australian Museum (AMS). The holotypes, some paratypes and some other representative specimens are in the South Australian Museum, Adelaide (SAM). A representative collection is housed in the United States National Museum of Natural History, Washington, D.C.

Methods: Series of 20–25 adult (occasionally more) snails were randomly selected from given samples for morphological analyses in the following manner. The sample was placed into a Petri dish, the bottom of which was divided into a grid of 50 equal-sized and numbered squares. A random number table was used to select grid squares. All adult snails, excluding highly eroded specimens, were removed from each selected square until the desired number of specimens was obtained. Shells were measured with either a Wild dissecting microscope (M5 or M7) fitted with an ocular micrometer, or with a Houston Instruments Hipad Digitizer linked to a Morrow Microdecision (MD2) computer. For measurements using the former method, a shell was first affixed to a piece of plastic clay, apex pointing directly upwards, so that protoconch diameter (PD, Fig. 4c) could be measured and counts made of protoconch and teleoconch whorls (PW, TW). The shell was then reoriented to the standard position, i.e. aperture facing upwards (Fig. 4a) and measurements made of shell height (SH), shell width (SW), aperture height (AH), aperture width (AW), and length of the body whorl (BW, Fig. 4a). For most shells measured using this method, a Wild M-5 microscope was used with 10× eyepieces, and 12× (large species) or 25× (small species) magnification for all shell features except protoconch diameter (50×). The variance in shell measurements using the ocular micrometer, as determined by repeated measurements of a given feature on a single specimen, was approximately 0.05 mm.

For measurements using the digitizing pad, shells were oriented in the positions described above and placed under a Wild M-5 dissecting microscope. The shell image was projected onto the digitizing pad by a drawing apparatus attached to the microscope. Shell features were measured by placing the cursor, equipped with a cross-hair, over standardized points of the shell in a predetermined sequence, with coordinate data sent to the computer at these points by pressing the cursor button, using the point, not stream, mode. In addition to the six meristic variables listed above, the width of the first half-whorl of

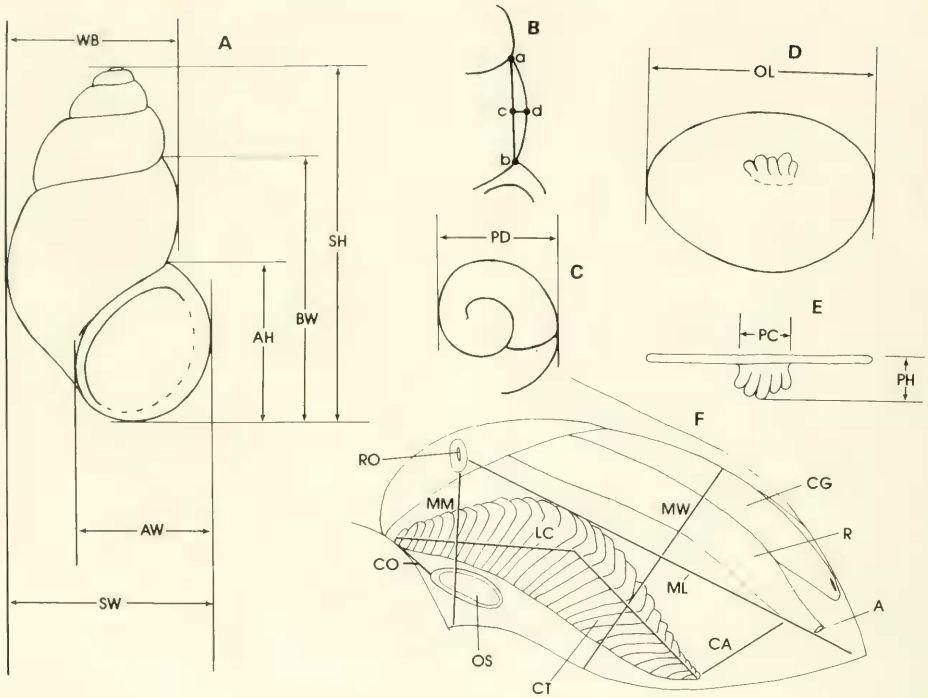

FIG. 4. Shell and operculum, showing various measurements.
A. Shell. AH, aperture height; AW, aperture width; BW, height of body whorl; SH, shell height; SW, shell width; WB, width of body whorl.
B. Shell showing measurements taken for convexity calculation (see methods).
C. Protoconch. PD, protoconch diameter.
D. Operculum, inner side. OL, opercular length.
E. Operculum, side view. PC, length of calcareous area; PH, peg height.
F. Pallial cavity, showing selected measurements of pallial structures.
A, anus; CA, distance from anus to ctenidium; CG, capsule gland; CO, distance between posterior end of osphradium and posterior end of ctenidium; CT, ctenidium; LC, length of ctenidium; ML, maximal length of pallial cavity; MM, minimal length of pallial cavity; MW, width of pallial cavity; OS, osphradium; R, rectum; RO, renal opening.

the body whorl (WB, Fig. 4a) and convexity of the penultimate whorl (CV; see below) were also measured using the Hipad. The Hipad was significantly more accurate than the above method, with repeated measurements varying by less than 0.02 mm. After a shell was measured it was cracked and the snail sexed by examination of the anterior portions of the genital tracts.

After sexing, opercula were removed from the same groups of snails used for shell measurements. Because measurements taken of the opercula of species of *Trochidrobia* did not provide useful data, these have been excluded from the analyses. The following methods apply to the opercula of species of *Fonscochlea*. Opercula were measured using a Wild M-5 dissecting microscope equipped with an ocular micrometer, with 10× eyepieces and 50× magnification. Opercula were first fixed flat onto a piece of plastic clay with the side that was attached to the foot facing upwards. The opercular length was measured (OL, Fig. 4d) and the calcareous pegs were counted. Then the opercula were stood on edge, with the pegs projecting beneath the operculum (Fig. 4e), enabling the length of the calcareous deposit (PC) and the height of the tallest peg (PH) to be measured.

Specimens were dissected after their shells were dissolved in Bouin's solution. Dissections were done while the animals were pinned out in a black wax-bottomed dish filled with a solution of 50–70% Bouin's solution

and water. Pallial and head structures were measured after the pallial roof and visceral coil were removed from the head/foot/neck. The digestive gland and gonad were then measured, followed by the other reproductive organs and stomach. All measurements were made, in the latter part of the study, with a crossed measuring reticule, divided into 200 segments on each line, in a 25× eyepiece using 31× magnification on the Wild M-7, or 25× magnification on the Wild M-5. In the early stages of the project a single line reticule, divided into 120 segments, in a 10× eyepiece, was used at 31× magnification on the Wild M-7. All measurements were converted into millimeters and used for calculation of ratios by the computer (see below).

The mean, standard deviation and variance were calculated for each attribute by sex for each population, using the microcomputer. All data files generated from the microcomputer were reformatted into data matrices based upon species and attribute groups and transmitted via a modem to disk storage on a mainframe computer, initially the CSIRO Cyber computer but more recently the NSW Data Processing Bureau Burroughs 7700. The Statistical Package for the Social Sciences was used to generate descriptive statistics (subprogram BREAKDOWN), test homogeneity of variances with both Bartlett's and Cochran's C-test, and perform two-tailed, single classification analyses of variance with the subprogram ONEWAY for each attribute. Missing data were ignored. In the cases in which groups of populations displayed significant heterogeneity of variance for given attributes, the data were transformed using either a log or arcsine transformation prior to analysis of variance. Student-Newman-Keuls test (SNK) and the Scheffe test were used to compare means using 0.05 and 0.001 probability levels. For all tests, significance was checked using the tables of critical values in Rohlf and Sokal (1969). Tests for sexual dimorphism were carried out using the subprogram ONEWAY on selected attributes for all species groups at probability levels of 0.05 and 0.001. Because some characters in some species proved to be sexually dimorphic, the male and female data were analysed separately.

Multivariate analysis was undertaken using discriminate function analysis (MDA) (hereafter referred to as discriminate analysis) using the BIOSTAT package of programs (Pimentel & Smith, 1986). Because there are problems in using ratios in multivariate analyses (Brookstein *et al.*, 1985) and closely correlated measurements a reduced set of measurements was used in the discriminate analyses [*Fonscochlea:* shell: SH, SW, AH, TW; operculum (not used with *F. zeidleri*): OL, PH, PC, PN; *Trochidrobia:* SH, SW, AH, AW, BW, TW, PD]. Discriminate analyses were run for each species group at the population level with sexes separate, and populations grouped into species and/or geographic forms of species with sexes separate and sexes combined. Anatomical data sets were run in the same way with two species groups in which anatomical data were used primarily to discriminate some of the species and geographic forms (*Trochidrobia* spp.; female genital measurements: GO, CG, AG, BC, WB, DB, CV, DV; "large aquatic" species of *Fonscochlea;* pallial measurements: LC, WC, FC, AC, HC, LO, WO, DO, CO, with sexes combined because of small numbers for each station).

Because of space constraints the univariate statistical analyses of the measurement data are not provided, nor are the details of the measurements obtained for every population. In the case of those data utilized in discriminate analysis, however, the results of an SNK test ($P<0.05$) are given for each character. It is hoped to utilize further the extensive set of measurement data in conjunction with a planned electrophoretic program. A summary of the measurement data is given in Appendix 2, Tables 18–21.

Characters: For descriptions of the taxa and analyses of morphological variation, the characters listed below were quantified for samples of snails from given populations.

The characters of the shell that were measured (Fig. 4A–C) are:

Maximal diameter of protoconch (PD).

Number of protoconch whorls (PW).

Number of teleoconch whorls (TW).

Shell height (SH), maximal length of shell along shell axis.

Shell width (SW), maximal width of shell perpendicular to shell axis.

Length of body whorl (BW), length from the suture, at junction of penultimate and body whorls.

Width of body whorl (WB), maximal diameter of first half-whorl of body whorl.

Height of aperture (AH), maximal length parallel to shell axis.

Width of aperture (AW), maximal width perpendicular to shell axis.

Convexity (CV), shortest distance from line

connecting sutures at junction between penultimate and body whorls to most abaxial point on whorl outline (Fig. 4B:c–d), divided by length of line connecting the two sutures (Fig. 4B:a–b).

The following ratios were generated from the shell measurements and used in the data analysis: protoconch diameter/shell height (PD/SH); shell width/shell height (SW/SH); aperture height/shell height (AH/SH); aperture height/length of body whorl (AH/BW); aperture width/width of body whorl (AW/WB); and an estimation of the degree to which the outer lip of the aperture protrudes beyond the outline of the junction of the penultimate and body whorl (WB/SW).

The opercular characters determined were:

Opercular length (OL), the maximal length of the operculum.

Number of opercular whorls (OW); determined for species of *Trochidrobia* only.

Number of pegs (PN) (i.e. number of separate calcareous projections); determined for species of *Fonscochlea* only, as were the following opercular characters.

Maximal height of pegs (PH), including thickness of operculum itself.

Length of calcareous smear (PC), length of calcareous deposit associated with pegs.

Several anatomical characters were determined. All measurements are maximal widths, lengths etc. unless otherwise stated. Characters of the head/foot and general body are:

Length of snout (LS), distance from eye to snout tip.

Length of tentacles (LT), distance from eye to tentacle tip.

Length of buccal mass (BM), measured after removal from snout.

Length of radular sac behind buccal mass (RS), length of portion of radular sac protruding from posterior end of buccal mass.

Length of digestive gland (LD), measured along its mid-upper surface following the coil.

Length of gonad (LG), measured as above.

Length of the digestive gland anterior to gonad (DG).

In the case of the pallial cavity all measurements were taken with the pallial cavity removed and flattened out (Fig. 4F). Characters are:

Maximal and minimal lengths of pallial cavity (ML, MM), distance from renal opening to given points along edge of cavity (Fig. 4F).

Width of pallial cavity (MW), taken as width of cavity approximately perpendicular to rectum (large species of *Fonscochlea*) (Fig. 4F) or as width along mantle edge (small species of *Fonscochlea,* and *Trochidrobia* spp.).

Number of ctenidial filaments (FC).

Length of ctenidium (LC), following curvature of ctenidium (Fig. 4F).

Width of ctenidium (WC), maximal width along long axis of filaments.

Gill apex (AC), width of ctenidium from left side to position of filament apex.

Filament height (HC), height of a filament at widest part of ctenidium.

Length and width of osphradium (LO, WO).

Distance between posterior tip of osphradium and posterior tip of ctenidium (CO) (Fig. 4F).

Shortest distance between osphradium and edge of pallial cavity (DO).

Distance between ctenidium and anus (CA), measured as shortest distance between anterior end of ctenidium and left side of anus (Fig. 4F).

Shortest distance between anus and mantle edge (MA).

Characters of the stomach are:

Length (SL), taken as entire length of stomach, including style sac, for *Trochidrobia* and small species of *Fonscochlea,* and length of stomach excluding style sac portion for large species of *Fonscochlea.*

Length of style sac (SS).

Height of anterior stomach chamber (AS).

Height of posterior stomach chamber (PS).

Many characters of the genital system were measured.

Whereas small variations due to reproductive state could not be assessed in this analysis, all individuals for which genital characters were measured appeared to be sexually mature. Immature or parasitized specimens were rejected.

Characters of the male genitalia are:

Length and width of prostate gland (PR, PW).

Length of pallial portion of prostate gland (PP), that part protruding into pallial cavity.

Length of penis (PL).

Characters of the female genitalia are:

Length of glandular oviduct (GO).

Length of capsule gland (CG) and albumen gland (AG).

Length of genital opening (GP).

Length and width of bursa copulatrix (BC, WB).

Length of duct of bursa copulatrix (DB).

Length and width of "seminal receptacle" (SR, WR), only for *Fonscochlea.*

Length of duct of "seminal receptacle" (DR), only for *Fonscochlea.*

Length of coiled portion of oviduct (CV), length of coiled section posterior to "seminal receptacle" *(Fonscochlea)* or bursa copulatrix *(Trochidrobia).*

Maximal and minimal diameters of coiled portion of oviduct (DV, MO).

Length of oviduct between seminal receptacle and bursa copulatrix (BS); *Fonscochlea* only.

Length of free portion of ventral channel (VC), that portion anterior to duct of bursa copulatrix.

For species of *Fonscochlea,* the following groups of anatomical ratios were used: a) pallial ratios: LC/SH (SH is shell height), LO/SH, FC/SH, MM/SH, HC/SH, MA/SH, CA/SH, MW/MM, LO/LC, HC/WC, AC/WC, WC/LC, WO/LO; b) general ratios: BM/SH, BM/RS, LT/LS, LD/SH, LG/LD; c) stomach ratios: SS/SL (see comments above under SL), PS/AS; d) male genital ratios: PL/SH, PP/SH, PP/PR; e) female genital ratios: AG/SH, CG/SH, CG/AG, BC/AG, DB/AG, SR/BC, CV/GO, VC/CV, VC/AG, BS/OD (OD = CV + VC), OV/GO (OV = CV + VC + BS). For *Trochidrobia,* the pallial ratios, stomach and general ratios, and male genital ratios were precisely the same as those for *Fonscochlea,* except that shell width (SW), rather than shell height, was used for scaling. The female genital ratios generated for *Trochidrobia* were AG/SW, CG/SW, CG/AG, BC/AG, DB/AG, CV/GO, VC/CV, VC/AG, DV/MO, DB/BC, and DV/VC.

Anatomy

Two species are described in detail, *F. accepta* (form A), from Welcome Springs, and *T. punicea,* from Blanche Cup Spring and Finniss Springs. Some supplementary information is given for *F. zeidleri* from Blanche Cup Spring.

The specimens were dissected by the same methods used to obtain the anatomical measurements above). Specimens fixed in Bouin's solution were sectioned in paraffin at about 6 microns and stained with Mallory's Triple Stain.

Physiology

Materials: The following snail species (with localities) were used in the experiments: *Trochidrobia punicea* (Finniss Springs), *Fonscochlea conica* (Welcome Springs), *Fonscochlea variabilis* form A (Blanche Cup, Coward Springs Railway Bore), *Fonscochlea accepta* form B (Finniss Springs), *Fonscochlea accepta* form A (Welcome Springs), *Fonscochlea aquatica* form A (Blanche Cup) and cf. form A (Kewson Hill) and *Fonscochlea zeidleri* form A (Finniss Springs, Blanche Cup, Kewson Hill and Coward Springs Railway Bore). These species represent the majority of those found in the southern and middle groups of springs found between Marree and Oodnadatta.

The springs from which the material studied was collected were, for logistical reasons, all in the southern half of the spring system between Marree and Oodnadatta (see Appendix 1 for detailed maps and station details). These were, in east-west order:

Welcome Springs (Stn 756), a moderately large spring with a low mound. A small pool near the head is a few cm deep and there is a shallow (< 1cm), rather long outflow. The substrate is a mixture of calcareous rock, sand and mud. Sedges are moderately common and filamentous algae are abundant.

Finniss Springs (Stn 693), a small spring with a very low sand mound. The substrate is sand and mud. Sedges are common and filamentous algae are present.

Blanche Cup Spring (Stn 739), a conical calcareous mound with a pool at the top (Fig. 1a). The outflow is shallow and mainly broad and flows over calcareous rock but the pool contains mainly mud. Sedges line the pool edges and filamentous algae are abundant in the pool and in the outflow.

Coward Springs Railway Bore (Stn 743), a very large swamp issuing from a large pond with the bottom composed mainly of silt. The water depth is generally in excess of several cm where the specimens were collected, in the vicinity of the pond outflow. Large sedges and rushes line the edges of the pool and outflow. Filamentous algae are abundant. This is the only known case in which the mound spring snails have become established in a bore drain. It is also the only known locality at which *F. zeidleri* is aquatic as well as amphibious. *Fonscochlea aquatica* is not found here and *T. punicea* is uncommon.

Kewson Hill Springs (Stn 742), one of several small springs issuing from this hill. They trickle down the steep hillside in narrow outflows where they form a series of small terraces (Ponder, 1986), each containing water a few mm deep. There is no vegetation apart from some filamentous algae.

Methods: All experiments were conducted in a makeshift laboratory set up in a large tent (5 × 4 m) in the field between August 27 and September 9, 1983. Snails from given populations were collected and then held in water in aerated plastic containers (16 × 16 cm) for one to three days before being used in the experiments. When possible, water from the spring from which a given sample of animals was collected was used for holding both the animals and for the experiments (Blanche Cup, Welcome Spring, Coward Springs Railway Bore). In instances in which a large water sample could not be obtained owing to shallow water and/or low discharge, water from a nearby spring or bore was used. In the case of Finniss Springs, the water was taken from a bore about 7 km southwest of Hermit Hill and the water used for the experiments with *F. aquatica* from Kewson Hill was taken from the Blanche Cup Spring. Full analyses of the water from these localities is given in Kinhill-Stearns (1984). A running record of the laboratory environment (air temperature, humidity) was kept. To avoid introducing age-related differences, only adult snails, i.e. those possessing a complete and thickened peristome, were used for the experiments.

A major problem encountered in physiological experiments involving shelled gastropods is determining when individuals are dead. Retraction of the snail into its shell usually occurs before death in response to unacceptable conditions. For most of the experiments the activity of the snails was used as an indicator of their tolerance to the conditions being presented. Given the time constraints inherent in the project, the customary replicates of each experiment could not be done. We preferred to use the available time to run each experiment for all of the taxa. The detailed methods of each type of experiment are given below.

In the desiccation experiments animals from given populations were placed in a series of 9-cm Petri dishes. Ten specimens were placed in each dish. The dishes were of three types: those lined with dry filter paper and without a lid (hereafter referred to as dry); those lined with moist filter paper and with a lid (moist); and those half-filled with water and with a lid (wet). The moist and wet tests served as controls. A total of 21 dishes, seven sets of each of the three types, was set up for each population tested. A separate set of dishes was checked after periods of one, two, four, six, 12, 24, and 48 hours from the beginning of the experiment. As the moistened dishes tended to dry out, despite having lids, they were frequently examined and re-moistened whenever necessary. To check for survival of snails in a set of dishes, the dishes were first flooded, if dry or moist, with water. The number of animals in each dish that were active 10 minutes after flooding was noted. A similar check for active animals was made one hour after flooding. Animals inactive after one hour were considered dead. Death was confirmed for the snails by tests carried out in some of the early runs: shells were gently crushed to expose the animal, placed under a dissecting microscope, and the mantle was not seen to retract when prodded.

In the salinity experiments table salt was added to the appropriate spring water to obtain solutions of six, nine, 12, and 24 ‰. The salinities of these solutions were tested using an optical refractometer. Each of these solutions, as well as a normal sample of the spring water, for which a zero salinity reading was obtained using the refractometer, serving as a control was added to a glass jar of about 380 cc brimfull capacity, which was then capped with a plastic lid to exclude air from the jar as much as possible. Ten specimens were placed into each of these five jars. After intervals of one, two, three, six, 12, and 24 hours, each of the jars was examined, but not opened, and the number of active or clinging snails counted. Mortality was not tested. The salinities for each of the water sources used, calculated from the conductivities given by Kinhill-Stearns (1984), are shown in Table 12.

In the experiments with deoxygenated water, water from the appropriate spring was boiled for two to three minutes in a glass beaker and then poured very gently, to prevent reoxygenation, into each of five 25 cc test tubes. Rubber stoppers were then gently inserted into each of the tubes. The tubes were cooled and then 20 snails were placed into each of them, as well as into a sixth tube containing well-oxygenated spring water as a control. The tubes were then again firmly stoppered, with an effort made to exclude air bubbles. After intervals of one, two, four, six, and 20 hours, a tube with deoxygenated water was checked in the following manner. First the number of active specimens in the tube was counted. Then the specimens from the tube were placed into a dish with oxygenated water. The number of active specimens in the dish was counted after periods of ten minutes and one hour. Specimens inactive after one hour

were considered dead. At the end of each of the five time periods, the control tube was examined as well, but not opened, and the number of active individuals in the tube counted.

The purpose of the temperature experiment was to determine activity of animals at various temperatures. Twenty specimens were placed into each of two 275 cc jars, half-filled with water. One jar was slowly heated by placing it into a steam-heated, water-filled dish. The jar was periodically removed from the water bath, the temperature of the water in the jar noted, and the number of active individuals in the jar counted when the desired temperatures were reached. The process was continued until such a temperature was reached at which all specimens became inactive. A similar method was used to determine tolerance to low temperatures: the second jar was placed into a small freezer and periodically removed to check the temperature and count the active animals. Again, the experiment was terminated when all specimens became inactive. The jars were not aerated during the experiments. Mortality was not tested and no attempt to achieve acclimation was made.

In determinations of submergence tolerance a 380 cc jar was filled to the brim with water and 20 snails were added. The jar was then capped with a lid that had a small hole in it so that an aerator tube could pass through it into the jar. An aerator stone was attached to the end of the tube. At intervals of one, two, four, 15, 24, 48, and 72 hours, the jar was examined and the number of active snails counted. In experiments of submergence/non-submergence preference a plastic plate was used (diameter of 220 mm), with a flat circular bottom (diameter of 150 mm), steeply-sloping sides (approximately 60° width of 13 mm), and a slightly-sloping rim (approximately 10° width of 22 mm). The dish was filled with water to the lower edge of the rim. Fifty snails were placed in the dish and left for three hours. At the end of this time period the numbers of specimens found on the bottom of the dish, on the steep slope and on the broad rim (out of the water) were counted.

In determinations of response to light a 200 × 200 × 15 mm clear perspex box, with tightly-fitting lid, was constructed for use in this experiment. Three lines were drawn across the width of the box in order to divide the box lengthwise into four equal zones. One hundred snails were placed in the box together with water. The water level in the box was then topped off and the lid placed on top, with a smear of petroleum jelly added to the sides to provide a seal. Care was taken to exclude any air bubbles from the box. Half of the box, containing two entire zones, was covered with a dark plastic sheet and then an Olympus dissecting microscope lamp was placed 2 cm above the mid-line at the uncovered end of the box. The lamp was oriented so that its beam was perpendicular to the plane of the box. The lamp was then turned on, to level 6 on the transformer, and the entire apparatus, box and lamp, was covered with a black plastic sheet to exclude other light. After one hour both the dark sheet and the sheet covering one half of the box were removed, and the numbers of animals in each of the four zones were quickly counted. The numbers of snails found in the light and light-middle zones were combined, as were those found in the dark and dark-middle zones, in order to obtain sufficiently high frequencies for the statistical analysis of these results. For most of the populations tested, two separate runs were done. The box was thoroughly washed and all grease removed between runs of this experiment.

To test for differences in results between runs, populations or species, the following statistical tests were used (following Siegel, 1956): Fisher's Exact Test, when the experiments involved fewer than 20 animals or when expected frequencies in cells were fewer than five; and The Chi-Square Test of Independence, with continuity correction, when the experiments involved 20 or more animals with expected frequencies in the cells exceeding five. Null hypotheses were rejected when the significance level was less than or equal to 0.05.

RESULTS

Taxonomy

The hydrobiids occurring in the Lake Eyre Supergroup are formally described in this section. Two new genera, *Fonscochlea* with six species and *Trochidrobia* with four species, are erected, with a new subgenus, *Wolfgangia,* of *Fonscochlea,* containing one species. Geographic forms are recognised in four of the species of *Fonscochlea,* these being formally described but not named.

A summary of measurement details is given in Appendix 2, Tables 18–21.

TABLE 2. Tests for sexual dimorphism in shell height (SH) and shell width (SW). The asterisk indicates a significant difference, at the level indicated, between males and females for all pooled measurements for the taxon.

	SH		SW	
Species	.05	.001	.05	.001
F. accepta form A	*	*	*	*
F. accepta form B	*	*	*	*
F. accepta form C				
F. aquatica form A	*	*	*	*
F. aquatica form B	*	*		
F. variabilis form A	*	*	*	*
F. variabilis form B	*	*	*	*
F. variabilis form C	*	*	*	*
F. billakalina			*	
F. conica	*	*	*	*
F. zeidleri form A			*	*
F. zeidleri form B	*	*		
T. punicea	*	*	*	*
T. smithi				
T. minuta			*	*
T. inflata				

Type species: *Fonscochlea accepta* n.sp.

Distribution: Artesian springs between Marree and Oodnadatta, northern South Australia.

Diagnosis: Shells (Figs. 5–7, 14, 19, 22, 23, 25) of known species small to large for family (1.3 mm long), non-umbilicate, ovate-conic to ovate, smooth or with weak axial rugae formed from enlarged growthlines. Protoconch (Fig. 9) of about one and one-half whorls, minutely pitted, the pits sometimes arranged into spiral rows (subgenus *Wolfgangia).* Aperture rather large relative to shell length (AH/SH >0.4), oval, thickened when mature, without external varix; outer lip slightly prosocline to slightly opisthocline. Periostracum thin, sometimes developing weak ridges that coincide with the growthlines and, sometimes, spiral scratches.

Operculum (Fig. 8) corneous, oval, flat, of few whorls, nucleus eccentric, inner surface with small calcareous smear and/or calcareous pegs.

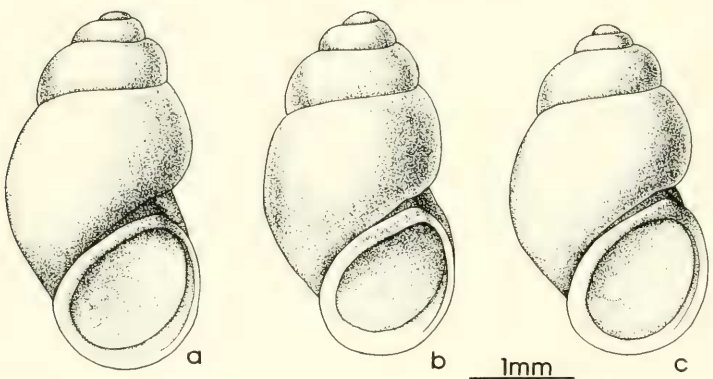

FIG. 5. Shells of *Fonscochlea accepta.*
a. *Fonscochlea accepta* form A, holotype. Welcome Springs (003).
b. *Fonscochlea accepta* form B. Old Finniss Springs (694) (SAM, D. 17918).
c. *Fonscochlea accepta* form C. Emerald Springs (703) (SAM, D. 17919).

Those species shown to be sexually dimorphic in size (at $P<0.01$) are listed in Table 2. Because most of the species showed evidence of dimorphism the morphometric data for each sex were treated separately. Some additional data are provided below.

Family Hydrobiidae

GENUS *FONSCOCHLEA* n. gen.

Derivation: *Fons* (Latin), a spring; *cochlea* (Latin), a snail (fem.).

Radula (Fig. 10) with rectangular central teeth, cusp formula $\frac{2-3+1+2-3}{1-2\ 1-2}$, lateral teeth 2−4+1+2−4. Inner marginal teeth with 8–15 cusps, outer marginal teeth with 17–25 cusps.

Head-foot (Figs. 11, 24a–g,i) typical of family. Cephalic tentacles slightly tapering to parallel-sided; weakly and inconspicuously ciliated on ventral surfaces. Snout well developed, slightly shorter to slightly longer than tentacles. Pigmentation heavy to light,

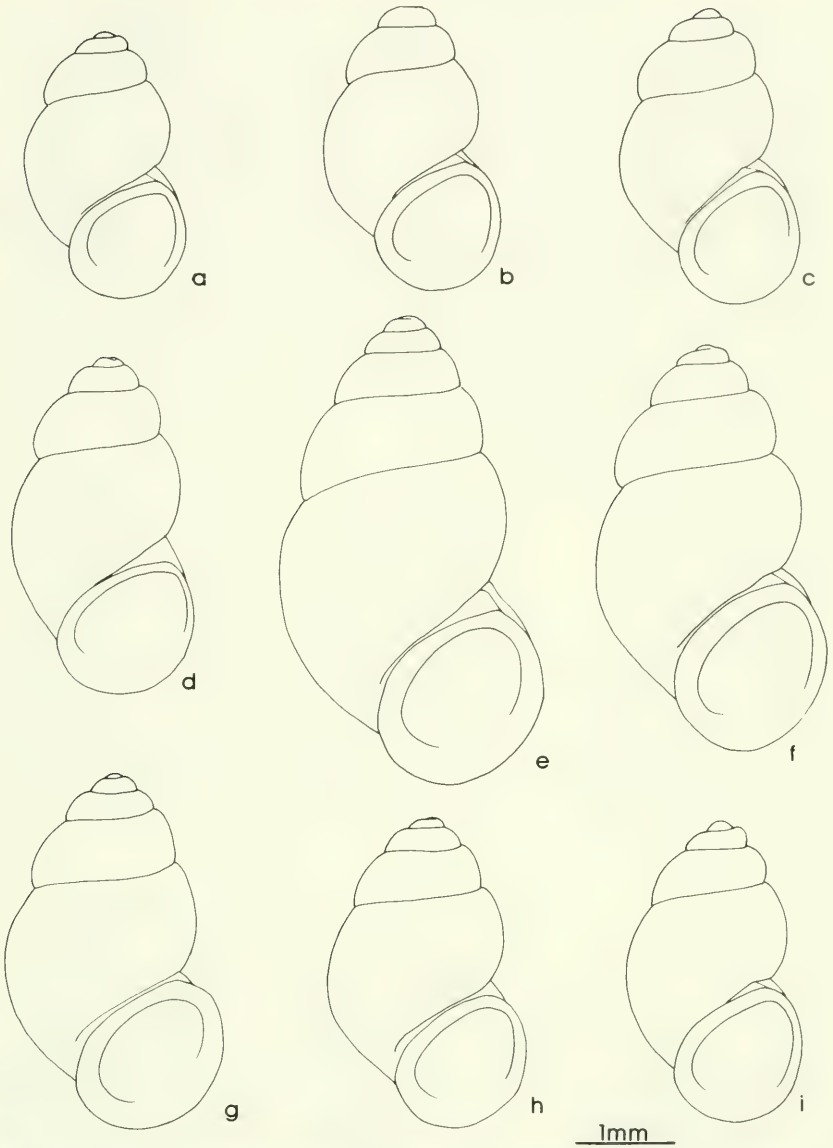

FIG. 6. Shells of species of *Fonscochlea*. a–d,i. *Fonscochlea accepta* form B. a. Finniss Swamp West (690)(AMS, C.152978). b. Sulphuric Springs (735) (AMS, C.152979). c. Hermit Hill Springs (711) (AMS, C.152980). d. Old Woman Spring (733) (AMS, C.152981). i. Old Finniss Springs (710) (AMS, C.152982). e–h. *Fonscochlea zeidleri* form A. e. Elizabeth Springs (024) (AMS, C.152975). f–h. Blanche Cup Spring (008) (AMS, C.152977).

pigment granules black and white. No accessory tentacles.

Pallial cavity (Fig. 4F) with well-developed ctenidium, osphradium oval, about three to four times as long as broad; its posterior extremity situated near posterior end of ctenidium. Ctenidium about 3–4.5 times length of osphradium.

Alimentary canal typical of family. Stomach (Figs. 43a, 44b, 45) with anterior and posterior chambers, single digestive gland opening and no caecal appendage.

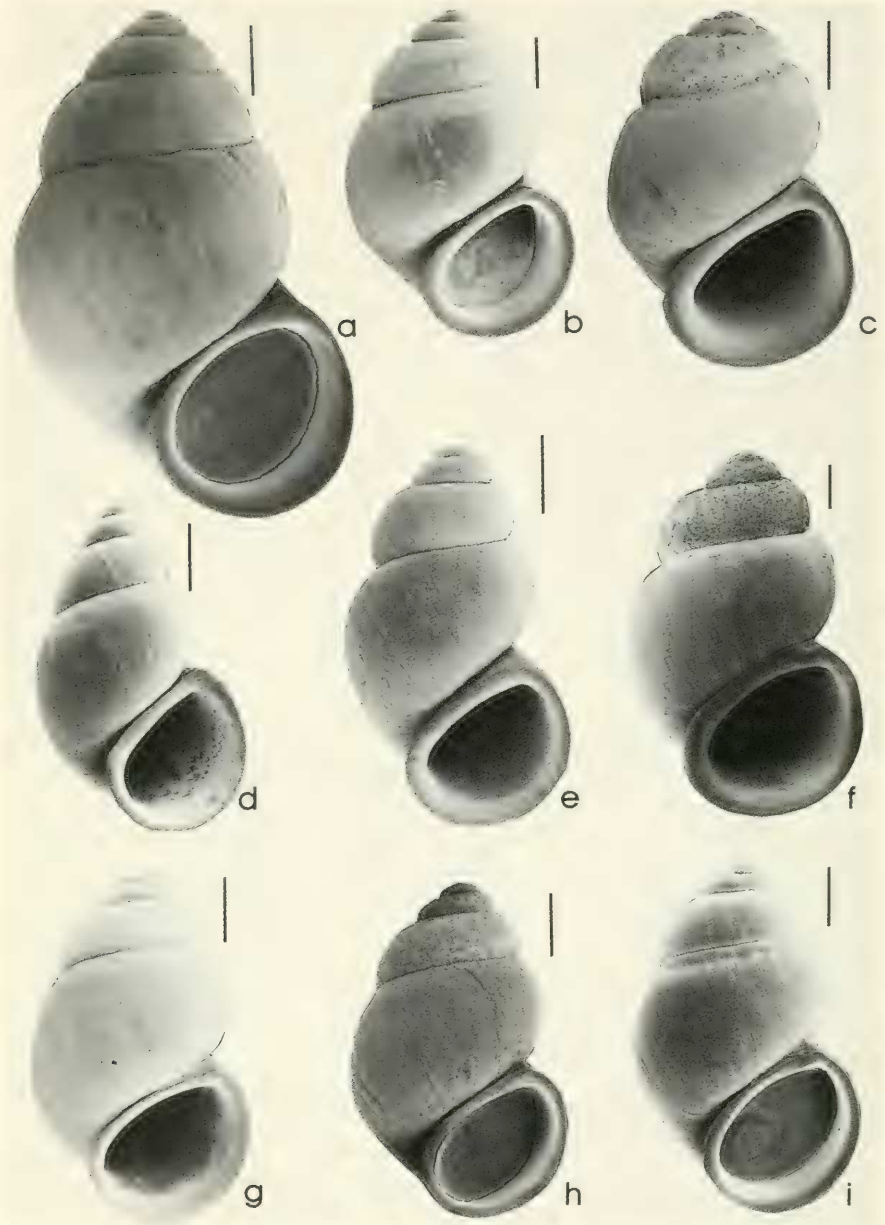

FIG. 7. Shells of species of *Fonscochlea.*
a. *Fonscochlea zeidleri* form A, Strangways Springs (030) (AMS, C.152992).
b. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661) (AMS, C.152993).
c. *Fonscochlea aquatica* cf. form A, very squat variety, Kewson Hill Springs (742) (AMS, C.152994).
d. *Fonscochlea billakalina,* paratype, Old Billa Kalina Spring (026) (AMS, C.152995).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032) (AMS, C.152996).
f. *Fonscochlea aquatica* form B, Freeling Springs (665) (AMS, C.152997).
g. *Fonscochlea accepta* form A, Welcome Springs (003) (AMS, C.152998).
h. *Fonscochlea accepta* form B. Old Finniss Springs (694B) (AMS, C.152999).
i. *Fonscochlea accepta* form C, Emerald Springs (703) (AMS, C.153000).
Scale: 0.5mm.

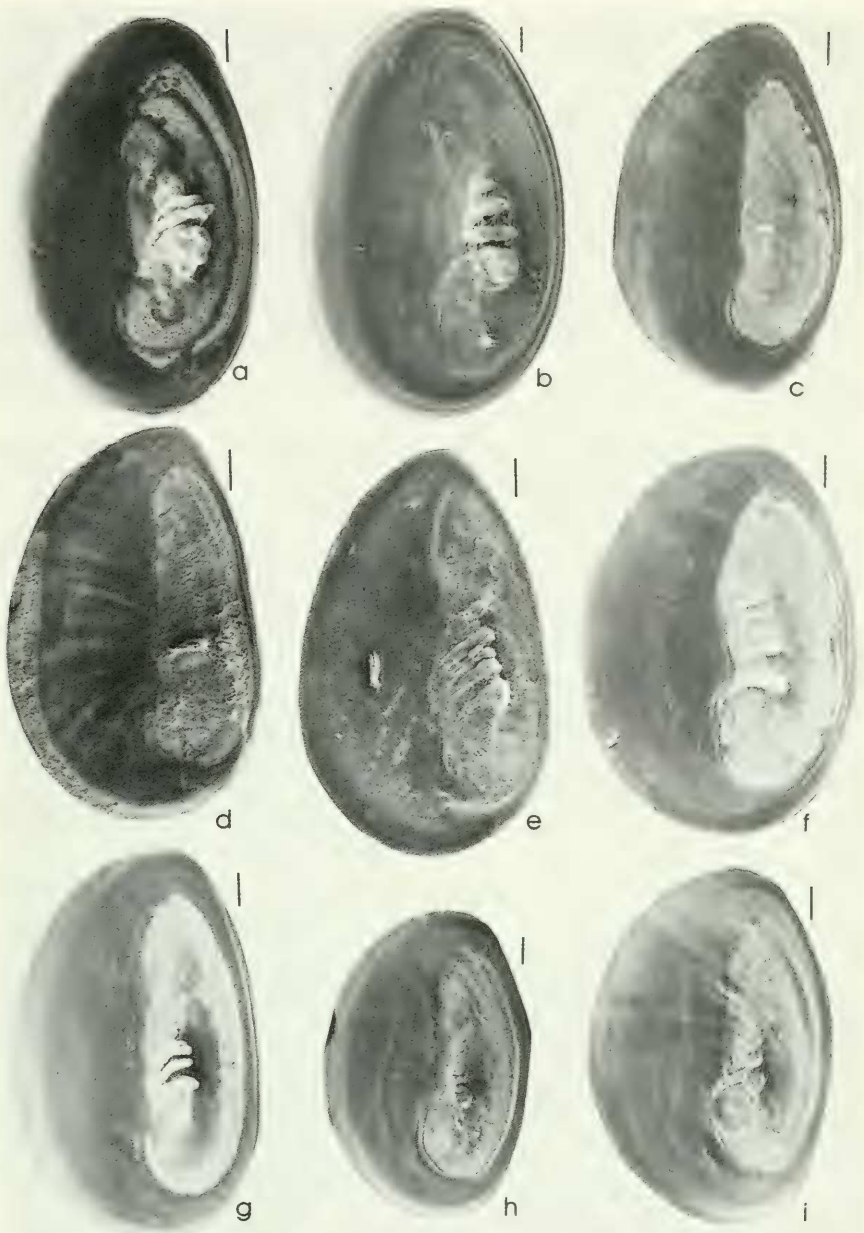

FIG. 8. Opercula of species of *Fonscochlea.*
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661).
b. *Fonscochlea zeidleri* form A, Coward Springs Railway Bore (018).
c. *Fonscochlea aquatica* cf. form A, Kewson Hill Springs (742).
d. *Fonscochlea billakalina,* Old Billa Kalina Spring (026).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032).
f. *Fonscochlea aquatica* form B, Freeling Springs (665).
g. *Fonscochlea accepta* form B, Old Finniss Springs (694B).
h,i. *Fonscochlea accepta* form A, Welcome Springs (003).
Scale: 0.1mm.

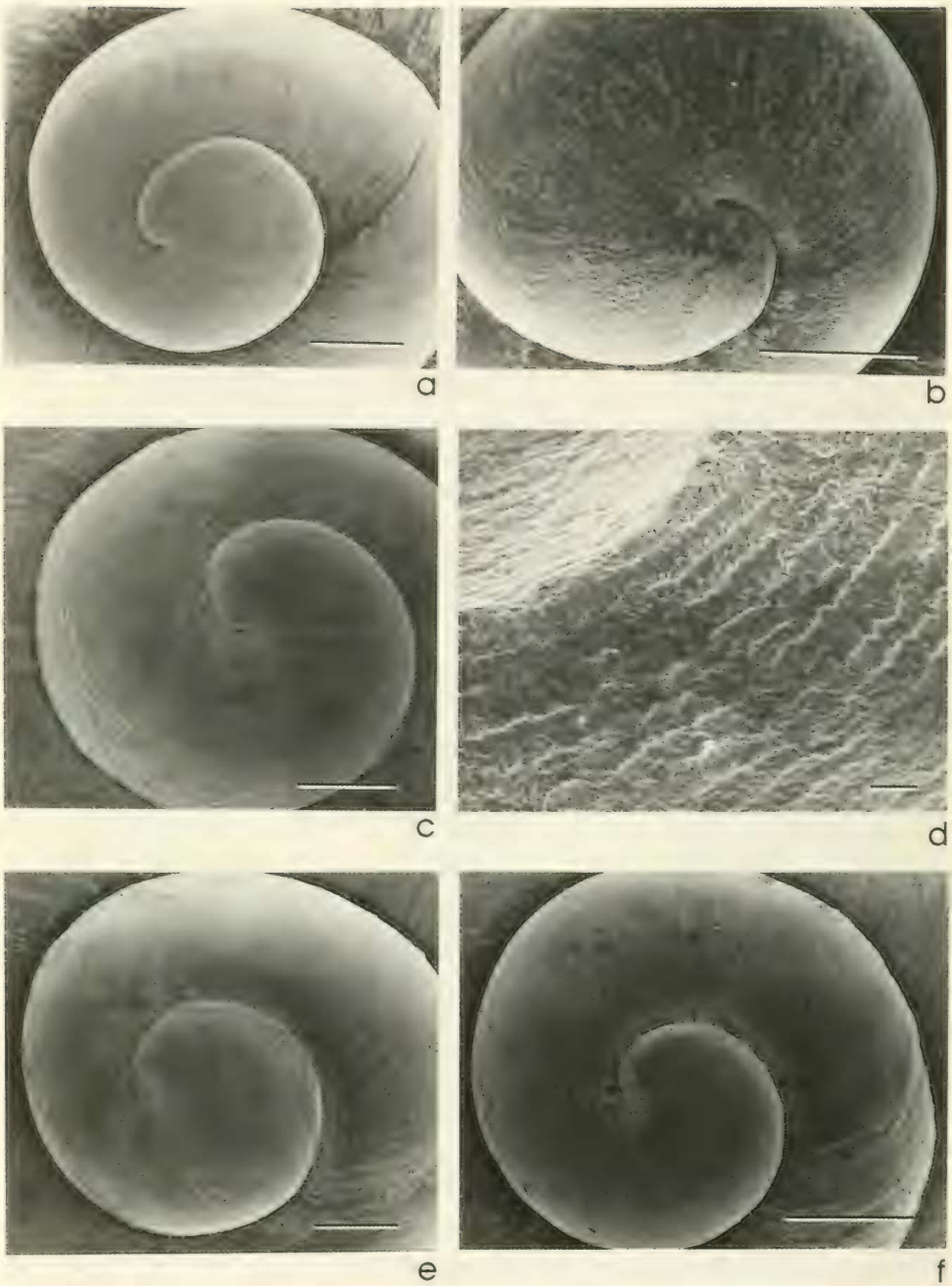

FIG. 9. Protoconchs of species of *Fonscochlea*.
a. *Fonscochlea accepta* form A, Welcome Springs (003).
b. *Fonscochlea accepta* form C, Emerald Springs (703).
c–d. *Fonscochlea zeidleri* form A, Strangways Springs (030).
e. *Fonscochlea aquatica* form A, Outside Springs (039).
f. *Fonscochlea conica*, Welcome Springs (003).
Scale: d = 0.01mm; all others = 0.1mm.

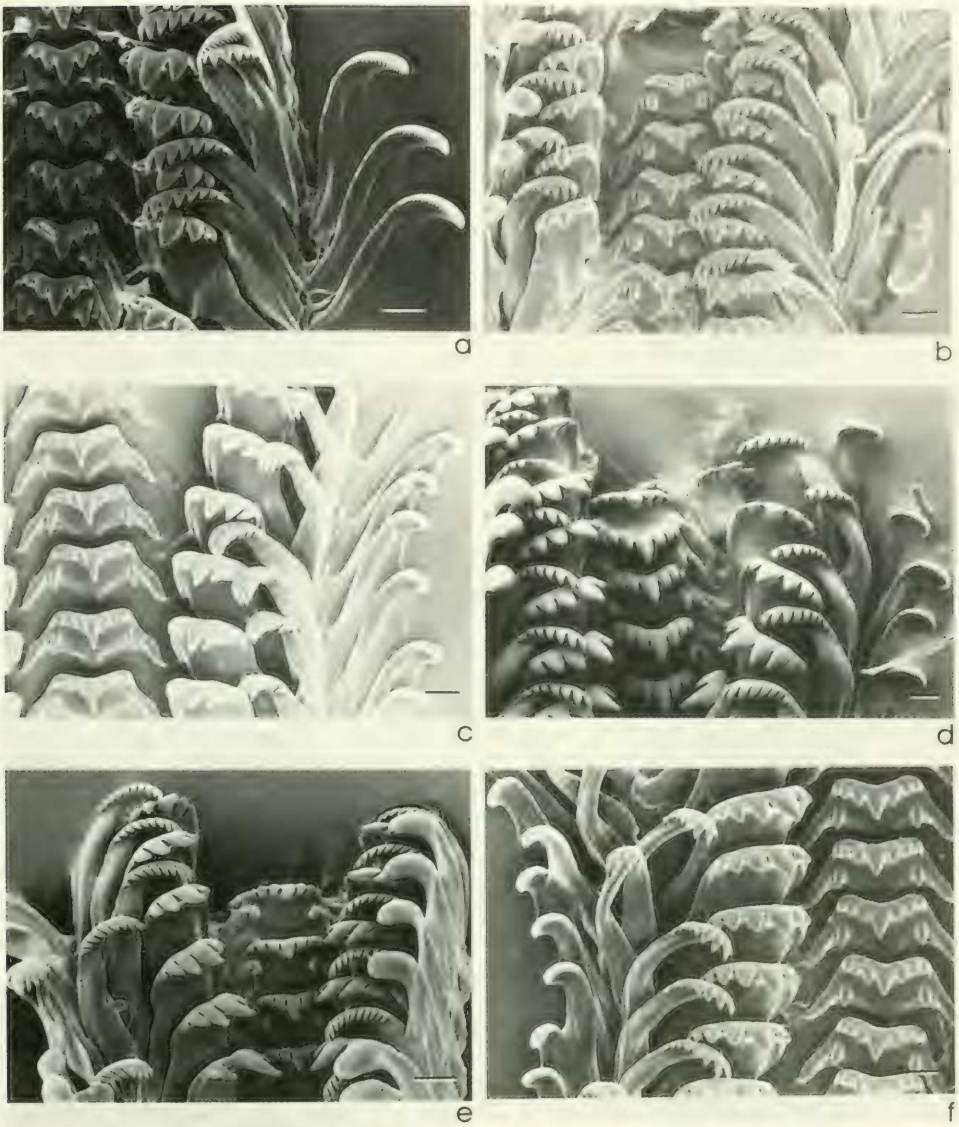

FIG. 10. Radulae of *Fonscochlea*.
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring (661).
b. *Fonscochlea zeidleri* form A, Coward Springs Railway Bore (018).
c. *Fonscochlea accepta* form B, Old Finniss Springs (694B).
d. *Fonscochlea accepta* form C, Emerald Springs (703).
e. *Fonscochlea variabilis* form B, The Fountain Spring (032).
f. *Fonscochlea aquatica* form B, Freeling Springs (665).
Scale: 0.01mm.

Female reproductive system (Figs. 12, 27, 47) with two sperm sacs, i.e. anterior bursa copulatrix and posterior "seminal receptacle", and coiled oviduct lying on inner (left) side of albumen gland, sperm sacs and major oviduct folds being opposite posterior part of gland or partly extending behind it. Coiled oviduct an unpigmented, coiled or undulating

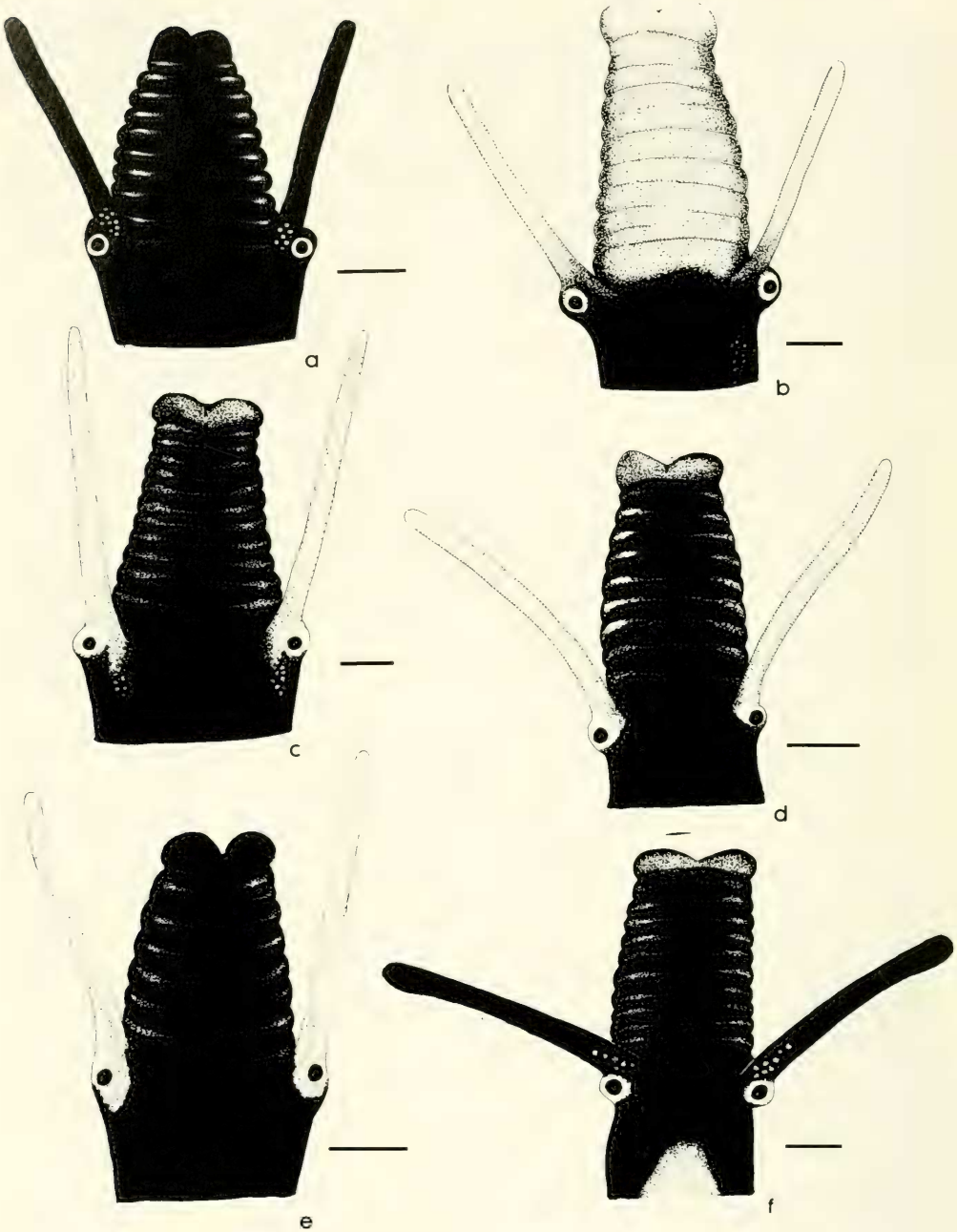

FIG. 11. Dorsal views of heads of large species of *Fonscochlea;* all from living material.
a. *Fonscochlea zeidleri* form A, Kewson Hill Springs.
b. *Fonscochlea zeidleri* form A, Welcome Springs.
c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
d. *Fonscochlea accepta* form A, Welcome Springs.
e. Fonscochlea aquatica cf. form A, Kewson Hill Springs.
f. *Fonscochlea accepta* form B, Old Finniss Springs.
Scale: 0.25mm.

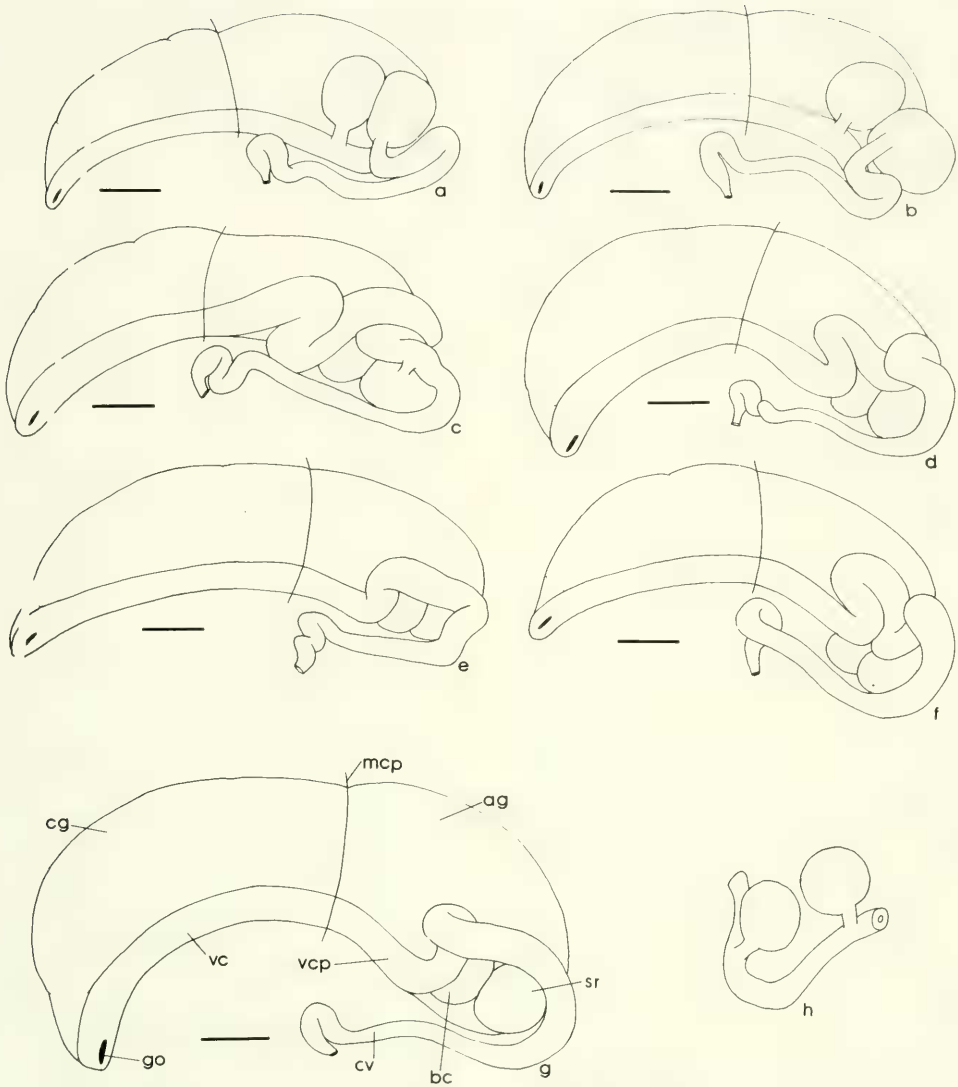

FIG. 12. Female genitalia of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form B, Big Cadnaowie Spring.
b. *Fonscochlea zeidleri* form A, Old Finniss Spring.
c. *Fonscochlea aquatica* form A, Blanche Cup Spring.
d. *Fonscochlea accepta* form A, Welcome Springs.
e. *Fonscochlea accepta* form C, Emerald Springs.
f. *Fonscochlea accepta* form B, Old Finniss Springs.
g,h. *Fonscochlea accepta* form A, Davenport Springs; detail of sperm sacs and their ducts shown in h.
ag, albumen gland; bc, bursa copulatrix; cg, capsule gland; cv, coiled oviduct; go, oviduct opening; mcp, posterior limit of pallial cavity; sr, seminal receptacle; vc, ventral channel; vcp, posterior extension of ventral channel.
Scale: 0.25mm.

muscular tube extending from immediately behind posterior pallial wall, where its initial section forms U-shaped, glandular loop, to loop posteriorly around sperm sacs at, or just behind, albumen gland. Gonopericardial duct represented by tissue strands only.

Oviduct between sperm sacs very short to moderately long, forming U-shaped loop. Anterior to bursal duct, which opens to oviduct opposite posterior part of albumen gland, muscular oviduct either runs straight to ventral channel or thrown into loop. Bursa copulatrix and "seminal receptacle" approximately equal in size and with ducts markedly shorter than length of sacs. Both sperm sacs similar histologically and rather thick-walled. Capsule gland approximately equal in size to albumen gland or slightly smaller or larger. Ventral channel well defined, with conspicuous ciliated lateral fold. Genital opening subterminal.

Male reproductive system with vas deferens complexly coiled beneath anterior part of testis. Pallial and visceral vas deferens enter and leave prostate gland in middle section. Prostate gland extends into pallial wall, as slight bulge in some species to about half its length in others. Pallial vas deferens narrow, tubular, and lying beneath epithelium of right side of pallial floor, undulating as it passes across neck and enters base of penis. Penis (Fig. 46) with swollen, unpigmented base bearing prominent concentric creases; distal two thirds smooth and tapering to point, often pigmented and muscular. Penial duct similar to pallial vas deferens, i.e. very narrow, ciliated and with only very thin muscle layer; straight in distal part of penis, undulating in proximal part. Penial pore simple.

Egg capsules hemispherical, attached to substrate.

Nervous system (Fig. 43b) with typical hydrobiid pattern: cerebral ganglia separated by short commissure, left pleural ganglion attached to suboesophogeal ganglion and right pleural ganglion separated from supraoesophageal ganglion by long connective.

See anatomical section below for further details of anatomy.

Remarks: The distinctive features of this genus include the equal-sized sperm sacs, the short ducts connecting these sacs to the oviduct and the position at which they enter the oviduct. In most hydrobiids the bursal duct opens to the oviduct opposite the anterior end of the albumen gland, not the posterior end as in *Fonscochlea*. The pegged operculum, and the shell of some of the smaller species, resemble states seen in the Australian species of *Hemistomia sensu lato* (Ponder, 1982). This genus, and the related genus *Tatea* T. Woods, 1879, can be distinguished from *Fonscochlea* in having a more "typical" hydrobiid reproductive system (Ponder, 1982). In these genera the seminal receptacle is thin-walled and much smaller than the bursa copulatrix, and the bursal duct opens to the oviduct in the region near the anterior end of the albumen gland. In most other respects these three genera are similar.

Subgenus *Fonscochlea s.s.*

Diagnosis: Shell (Figs. 5, 6a–d, i, 7c–i, 14b, d, 19, 22, 23, 25) thin to moderately thick, aperture with thin to slightly thickened peristome. Protoconch microsculpture (Fig. 9a,b,e,f) of irregular, shallow pits.

Operculum (Fig. 8c–i) with prominent pegs, weak pegs or pegs absent.

Radula (Fig. 10c–f) as for genus. (Table 3)

Head-foot (Figs. 11c–f, 20a–g, i) with cephalic tentacles slightly longer than snout.

Female genital system (Figs. 12c–h, 27) as for genus except that the oviduct between the ventral channel and the bursal duct is always bent or folded and the sperm sacs lie behind (to the right of) the coiled oviduct and their ducts emerge from their dorsal sides.

Male system as for genus.

Remarks: The typical subgenus includes five of the six known taxa of *Fonscochlea*. It encompasses two radiations, one of small species and the other of large species, all of which are aquatic.

Group 1: the large aquatic species.

Fonscochlea accepta n.sp.

Derivation: *accepta* (Latin), welcome, a reference to the type locality.

Diagnosis: Shell about 2.4 to 3.8 mm long, with about 2.5–3.6 convex (convexity ratio 0.08–0.25) teleoconch whorls. Aperture with thin peristome, outer lip slightly prosocline. Inner lip narrow, loosely attached to parietal wall. Operculum with strong pegs.

Shell (Figs. 5, 6a–d,i, 7g–i; 9a,b), see diagnosis. Colour dark brown.

Operculum (Fig. 8g,i) with several, usually 3–4, strong pegs.

Radula (Fig. 10c,d) as for genus (see Table 3 for details).

Head-foot (Fig. 11d,f), see under descriptions of the forms of this species below.

Anatomy typical of subgenus. Described in more detail in the anatomical section below.

The typical form of this species is described

TABLE 3. Cusp counts from radular teeth of species of *Fonscochlea* and *Trochidrobia*. Missing counts from the outer marginal teeth are the result of not being able to make accurate counts from the available preparations.

Species	Central tooth		Lateral tooth		Inner marginal tooth	Outer marginal tooth
	No. of lateral cusps	No. of basal cusps	No. of inner cusps	No. of outer cusps	No. of cusps	No. of cusps
F. accepta form A	3–4	1	3–4	3–4	9–10	24–25
F. accepta form B	3	1–2	2–3	3–4	9–12	—
F. accepta form C	4	1–2	3	3–4	10–13	—
F. aquatica form A	3–4	1	2–3	2–4	7–10	—
F. aquatica form B	2–3	1	3	3	8–9	21–25
F. variabilis form A	4–6	1–2	2–3	2–4	12–15	—
F. variabilis form B	3–4	1–2	2–3	2–3	9–12	—
F. variabilis form C	2–4	1–2	2	2–3	9–11	—
F. billakalina	3–4	1–2	2–3	2–4	10–12	—
F. conica	4–6	1–2	3	3–4	14–18	—
F. zeidleri form A	2–3	2	2–3	3	9–13	17–21
F. zeidleri form B	2–3	2	2–3	3	9–10	20–21
T. punicea	5–8	1–2	3–6	4–6	24–31	—
T. smithi	6–7	1	4–5	5–6	23–25	—
T. minuta	4–7	1–2	4–6	6–7	22–24	—
T. inflata	6–8	1	5–6	5–7	18–23	—

below as "form A" where a holotype is designated for the species.

Localities: Southern Springs: Welcome, Davenport, Hermit Hill and Emerald Springs (Fig. 13).

Remarks: Three geographically separated forms are recognised. Discriminate analysis did not convincingly separate two of these using shell and opercular characters but reasonable discrimination was achieved using pallial data. The forms are primarily distinguished by differences in their ctenidia and unquantified differences, including tentacle shape and pigmentation and habitat preference.

This species has a range of about 80 km with the typical form occupying about a 25 km range, separated from the Hermit Hill populations (form B) by about 12 km and those in turn separated from Emerald Spring, the locality of the third form, by about 40 km.

This species is the "large aquatic" species of the Southern Springs. It is generally abundant in the pool at the head of the springs and in their outflows. It can sometimes be seen clustering on the sides of the outflows but it is not amphibious and, if emergent, is covered by a film of water.

Fonscochlea accepta form A.

(Figs. 5a, 7g, shell; 9a, protoconch; 8h,i, operculum; 11d, head-foot; 43a, 44b, stomach; 43b, nervous system; 46a, penis; 12d,g,h, female genitalia.

Diagnosis: Tends to have longer and more numerous ctenidial filaments (Table 18B) than *F. accepta* form B and shorter filaments than *F. accepta* form C. Radular sac longer, and ratio of buccal mass to radular sac (BM/RS) smaller, than in both other forms. Also differs from *F. accepta* form B in pigmentation and morphology of cephalic tentacles.

Shell (Figs. 5a, 7g; 9b, protoconch) as for species, but not so broad relative to length as *F. accepta* form C. See Table 18A for measurement data.

Operculum (Fig. 8h) as for species. See Table 18A for measurement data.

Radula as for species. See Table 3 for data.

Head-foot (Fig. 11d) black on sides of foot and on neck and snout. Tentacles parallel-sided or taper slightly distally and lightly to darkly pigmented, except for pale median stripe most obvious in individuals with darker tentacles. An indistinct red-brown patch on outer dorsal side of tentacles just in front of eyes present and few dense white pigment cells lie above eyes.

Anatomy (Figs. 12d,g,h, female genitalia; 43a, 44b, stomach; 43b, nervous system; 46a, penis) as for species. See Tables 18B–E for measurement data.

Type material: holotype (Fig. 5a) (SAM, D.17917, stn 003); and paratypes (003, AMS,

FIG. 13. Distribution of large aquatic species, *Fonscochlea accepta*, *F. aquatica*.

C.152848, many, C.152998, 1, figured; 756A, AMS, C.152849, many; 756B, AMS, C.152850, many; 756C, AMS, C.152851, many).

Dimensions of holotype: length 3.26 mm, width 1.83 mm, length of aperture 1.43 mm.

Localities: Welcome Springs (002, 003, 754A–D, 755A–D, 756A–C); Davenport Springs (004, 005, 752A,C, 753A,B (Fig. 13).

Remarks: The populations at Welcome and Davenport Springs do not seem to show any significant differences in any of the non-genital characters measured but there are some differences in measurements in the female genitalia. In particular BS/OD, CV/GO and OV/GO are significantly different. It is possible, on more detailed analysis, that these populations, which are more than 20 km apart, will be shown to be separable.

Fonscochlea accepta form B.

Figs. 5b, 6a–d,i, 7h, shell; 11f, head-foot; 12f, female genitalia; 8g, operculum; 10c, radula

Diagnosis: Ctenidial filaments fewer and shorter than in other two forms, and ctenidium tends to be shorter, although these differences not consistently significantly different for all populations. Radular sac shorter, and ratio of buccal mass to radular sac (BM/RS) larger, than in both other forms of *F. accepta.* Cephalic tentacles with reduced or absent median stripe and not tapered.

Shell (Figs. 5b, 6a–d,i, 7h) generally similar to form A but some individuals approach *F. accepta* form C in shape. See Table 18A for measurement data.

Operculum (Fig. 8g) as for species. See Table 18A for measurement data.

Radula (Fig. 10c) as for species. See Table 3 for data.

Head-foot (Fig. 11f) similar to that of *F. accepta* form A but median stripe on tentacles reduced or absent and tentacles usually slightly swollen distally, or if not, parallel-sided (i.e. not tapered).

Anatomy (Fig. 12f) as for species. See Tables 18B–E for measurement data.

Voucher material: primary voucher specimen (Fig. 5b) (SAM, D.17918, stn 694B); additional material from same station (694B, AMS, C.152852, many, C.152999, 1, figured; 693A, AMS, C.152853, 36; 693B, AMS, C.152854, 50; 693C, AMS, C.152855, 10; 694A, AMS, C.152856, 10; 694C, AMS, C.152857, 16).

Dimensions of primary voucher specimen: length 3.17 mm, width 1.86 mm, length of aperture 1.38 mm.

Localities: Hermit Hill Complex: Hermit Hill Springs (711A–D, 712); Old Finniss Springs (693A–C, 694A–C, 710); Old Woman Springs (733A–E); Finniss Swamp West (690A–C, 691A–D, 730); Dead Boy Spring (689); Sulphuric Springs (735); Bopeechee Springs (692A,B). Shells, possibly referable to this form, are known from Priscilla (686) and Venable (687) Springs (Fig. 13).

Remarks: This form is distinguished from *F. accepta* form A in ctenidal characters, a shorter radular sac, and tentacle shape. The smaller gill seen in *F. accepta* form B might have evolved in response to the generally small springs found in the Hermit Hill area. This form also differs behaviourly from form A, preferring the shallow water in the outflows to the deeper water in pools, whereas *F. accepta* form A is found in pools in large numbers.

Using discriminate analysis on a subset of shell measurements and opercular measurements, populations of this form did not separate well from *F. accepta* form A, although partial separation is achieved (Figs. 15, 16; Table 4). Pallial measurements, however, produced a clear separation from form A and the next form (Figs. 17, 18; Table 4).

Fonscochlea accepta form C.

(Figs. 5c, 7i, shell; 9b, protoconch; 10d, radula; Fig. 12e, female genitalia)

Diagnosis: Shell with relatively shorter spire than many other populations, but this not consistent. Gill filaments longer, typically twice as long, and more numerous than those of *F. accepta* form B. Similar, but less pronounced, differences between this form and *F. accepta* form A, with ratios of ctenidial length/shell length (LC/SH) and length of ctenidial filaments to shell length (HC/SH) larger than in both other forms. Distance between anus and ctenidium (CA) and ratio of this distance over shell length (CA/SH) larger than in other two forms. Radular sac intermediate in length between other two forms. Head-foot (not observed in living material) similar to *F. accepta* form A in having well-developed, unpigmented dorsal stripe on tentacles.

Shell (Figs. 5c, 7i; 9b, protoconch) as for species except for a relatively larger aperture (mean of AH 1.52, males; 1.51, females; compared with 1.31–1.46 mm for the other two forms). AH/BW is larger in most individuals than in the other two forms (mean 0.62, com-

TABLE 4. Summary of results of discriminate analysis of the forms of the large aquatic species of *Fonscochlea*. The numbers are the Euclidean (taxonomic) distances between the groups.

	*F.ac.*A	*F.ac.*B	*F.ac.*C	*F.aq.*A	*F.aq.*A(r)	*F.aq.*cf.A	*F.aq.*B	
F. accepta form A	X	0.460	0.598	1.611	1.477	2.519	1.010	Right side: Female, shell & operculum
		0.470	0.131	1.472	1.274	2.693	1.042	Male, shell & operculum
F. accepta form B	0.459	X	0.503	1.762	1.742	2.418	1.302	
	0.198		0.442	1.570	1.521	2.517	1.229	
F. accepta form C	0.375	0.370	X	1.286	1.328	1.964	0.950	
	2.722	2.889		1.484	1.298	2.685	1.063	
F. aquatica form A	1.550	1.667	1.326	X	—	—	0.771	
(combined)	—	—	—		—	—	0.521	
F. aquatica form A	1.384	1.630	1.272	—	X	1.842	0.507	
(restricted)	9.365	9.533	6.756	—		2.119	0.372	
F. aquatica cf. form A	2.606	2.463	2.261	—	1.972	X	2.029	
	0.396	0.539	2.402	—	—		2.020	
F. aquatica form B	1.025	1.253	0.901	0.637	0.420	2.004	X	
	3.630	3.797	1.169	—	5.737	3.271		

Left top—shell + operculum combined sexes
Left bottom—pallial combined sexes

pared with 0.57–0.58). See Table 18A for measurement data.

Operculum as for species. See Table 18A for measurement data.

Radula (Fig. 10d) as for species. See Table 3 for data.

Head-foot similar to that of *F. accepta* form A as far as can be judged from preserved material.

Anatomy (Fig. 12e, female genitalia) as for species. See Tables 16B–E for measurement data.

Voucher material: primary voucher specimen (Fig. 5c) (SAM, D.17919, stn 703A); additional material from same station (703A, AMS, C.152858, many, C.153000, 1, figured; 703B, AMS, C.152859, 60).

Dimensions of primary voucher specimen: length 3.10 mm, width 1.90 mm, length of aperture 1.40 mm.

Locality: Emerald Springs (703A,B).

Remarks: This population is recognised as a separate form because it differs from the other two forms, particularly *F. accepta* form B, in gill characters, as described above. It appears to have head-foot characters similar to those of *F. accepta* form A, but differs from *F. accepta* form B in this respect, and also differs in the distance of the anus from the mantle edge from both of the other forms. Discriminate analysis on pallial measurement data readily separates this form (Figs. 17, 18; Table 4).

This form lives in the upper outflow of a large, isolated spring in swiftly flowing water that reaches a depth of as much as several centimeters. It is common in the roots of dense vegetation around the fenced spring head at the uppermost part of the outflow but relatively rare on the downstream side of the fence where it appears to require shelter beneath debris such as wood. This suggests that, unlike the other two forms, which are commonly seen in the open, this form is strongly photonegative.

Emerald Springs is unusual in containing only one species of hydrobiid. This locality is widely separated, by about 40 km, from other populations of *F. accepta,* the nearest being those in the vicinity of Hermit Hill (*F. accepta* form B).

Fonscochlea aquatica n.sp.

Derivation: a reference to the aquatic habit of this species, in contrast to *F. zeidleri.*

Diagnosis: Shell large for genus (2.6 to 4.8 mm long), with 2.1–3.7 teleoconch whorls. Aperture with thin peristome and orthocline to opisthocline outer lip. Inner lip broad and firmly attached to parietal wall. Operculum with weak or absent pegs.

Shell (Figs. 7c,f; 14b,d; 53c,e; 9e, protoconch) as for diagnosis. Colour yellowish-brown to chocolate or reddish-brown.

Operculum (Fig. 8c,f) with pegs weak to moderately strong, or absent altogether.

Radula (Fig. 10f) as for genus. See Table 3 for details.

Head-foot (Figs. 11c,e) with pale, tapering cephalic tentacles and the darkly-pigmented head and snout.

Anatomy (Fig. 12c, female genitalia) typical of subgenus. Similar to *F. accepta,* differences being mainly size-related.

The typical form of this species is described below as "form A" where a holotype is designated for the species.

Localities: Middle, South Western, Northern and Freeling Springs (Fig. 13).

Remarks: This species can be divided into two geographic forms, possibly subspecies, which are separated on shell and opercular characters. It differs from *F. accepta* in its larger size (SH) and most other shell measurements are significantly different in nearly all populations and, consequently, many other size-related characters. They also differ in apertural details and in the relatively weaker to absent pegs on the operculum; PH/OL, PC/OL and PN/OL are all significantly different in most populations. The ratio AH/BW (aperture height/body whorl) is significantly larger in *F. aquatica* than in *F. accepta* in nearly all populations. This species separated well from *F. accepta* in discriminate analysis using shell and opercular measurements (Figs. 15, 16; Table 4).

Fonscochlea aquatica form A.

(Figs. 7c, 14d, 53c,e, shell; 9e, protoconch; 8c, operculum; 11c,e, head-foot; 12c, female genitalia)

Diagnosis: Shell with 2.10–3.63 (mean 3.24, males; 3.26, females) weakly to moderately convex teleoconch whorls (convexity ratio 0.16–0.24; mean 0.17, males; 0.18, females). Aperture oval with inner lip attached to parietal wall over most of length. Colour yellowish to chocolate brown. Operculum with calcareous smear 0–0.4 mm long (mean 0.22 mm, males; 0.21, females).

Shell (Figs. 7c, 14d, 53c,e; 9e, protoconch) as for diagnosis. See Table 18A for measurement data.

Operculum (Fig. 8c) with 1–4 (mean 2.80, males; 2.57, females) pegs, 0.02–0.29 mm (mean 0.10 mm, males; 0.11 mm, females) high. See Table 18A for measurements.

Radula as for species. See Table 3 for data.

Head-foot (Fig. 11c,e) as for species; dorsal cephalic tentacles uniformly lightly to darkly pigmented, sometimes with narrow, short unpigmented stripe bordered with dark lines.

Anatomy (Fig. 12c, female genitalia) as for species. See Tables 18B–E for dimensions.

Type material: holotype (Fig. 14d) (SAM, D.17920, 009); and paratypes (008, AMS, C.152860, 2; 685, AMS, C.152861, many; 739, AMS, C.152862, many).

Dimensions of holotype: length 4.27 mm, width 2.45 mm, length of aperture 1.86 mm.

Localities: Middle Springs: Horse Springs East (747A,B, 748A–C), Horse Springs West (746A,B), Mt. Hamilton Homestead (006), Strangways Spring (745A), Blanche Cup Spring (008, 685,739), Little Bubbler Spring (744A–C), Bubbler Spring (013), unnamed springs, Blanche Cup Group (786, 787), Coward Springs (019, 764A–C), Kewson Hill Springs (740, 741, 742A,B, 765), Elizabeth Springs (766A–F, 767A,B, 771A–C), Julie Springs (772A–D, 773A,B), Jersey Springs (683A,B, 769A,B, 770A), Warburton Spring (681A–C, 682), Beresford Spring (028).

South Western Springs: Billa Kalina Springs (026, 723A–D, 759A, 761A–C, 762A,B, 763A,B), Francis Swamp (717B,C, 720A,B, 721A–C), Strangways Springs (007, 029–030, 678A,B, 679A–C). Shells only from Margaret Spring (722).

Northern Springs: Brinkley Springs (677), Hawker Springs (670B,C, 671, 672A–D, 673), Fountain Spring (031–033), Twelve Mile Spring (036,037), Big Perry Spring (034), Outside Springs (038–040, 041) (Fig. 13).

Remarks: This form is the large aquatic species living in the Middle, South Western and Northern Springs, replacing *F. accepta,* which occurs in the Southern Springs.

Specimens from the Kewson Hill Springs and, to a lesser extent Elizabeth, Jersey and Julie Springs, tend to have stunted shells (Figs. 7c, 53c) and smaller gills with fewer filaments than have other populations of this form. The only important characters consistently separating these populations are peg height (PH) and the length of the calcareous smear (PC) and these, together with the values of PH/OL and PC/OL, are significantly different from those of all other populations of *F. aquatica.* Peg number also tends to be less, but not consistently so. The non-opercular dif-

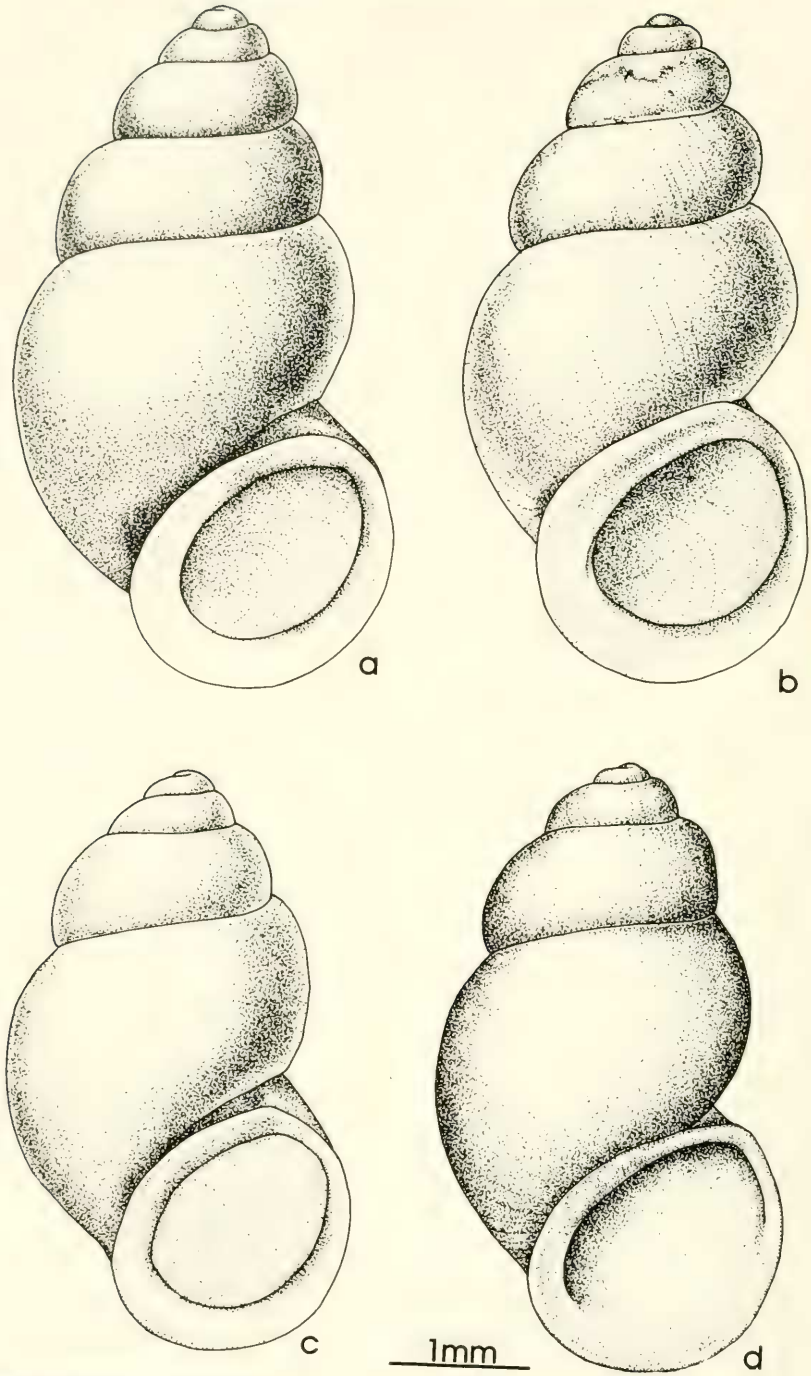

FIG. 14. Shells of species of *Fonscochlea*.
a. *Fonscochlea zeidleri* form A, holotype. Coward Springs (764).
b. *Fonscochlea aquatica* form B. Freeling Springs (665) (SAM, D.17921).
c. *Fonscochlea zeidleri* form B. Big Cadnaowie Spring (661) (SAM, D.17916).
d. *Fonscochlea aquatica* form A, holotype. Blanche Cup Spring (009).

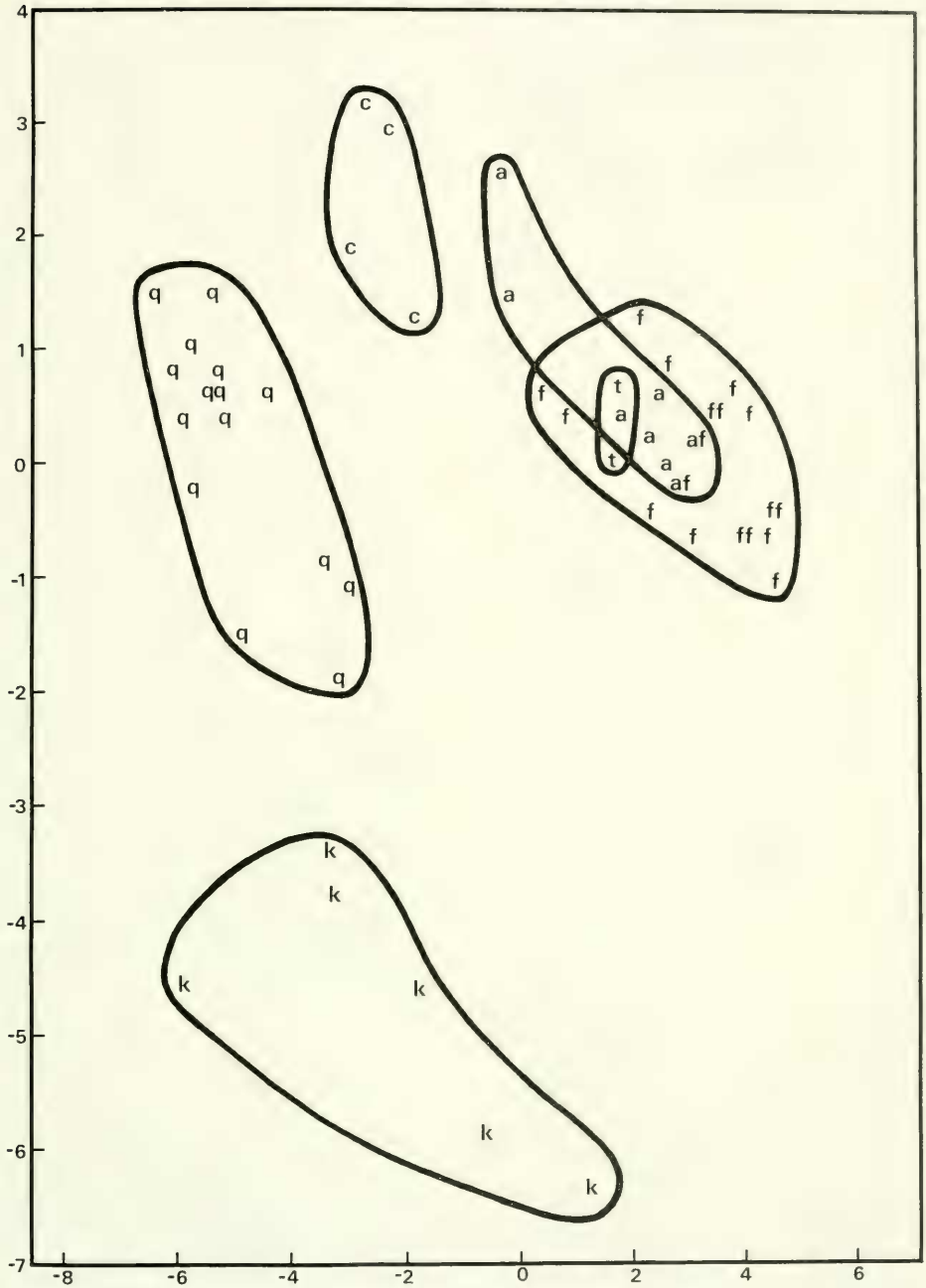

FIG. 15. Plot of group centroids, using the first two canonical axes, obtained from discriminate analysis of populations of large aquatic species and forms of *Fonscochlea* using shell and opercular measurements. Males and females of each population are, for the purposes of this analysis, treated as distinct populations. The axes contain the following percentages of the variance of the variables used: first (horizontal) axis: SH, 50.15%; SW, 41.40%; AH, 74.33%; TW, 53.49%; OL, 91.57%; PH, 78.06%; PC, 35.01%; PN, 38.94%. Second (vertical) axis: SH, 0.18%; SW, 19.15%; AH, 6.39%; TW, 2.14%; OL, 4.03%; PH, 13.72%; PC, 47.09%; PN, 0.06%. a, *F. accepta* form A; c, *F. aquatica* form B; f, *F. accepta* form B; *k*, *F. aquatica* cf. form A; q, *F. aquatica* form A, typical; t, *F. accepta* form C.